AUTHOR'S ABSTRACT OF THIS PAPER ISSUED
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THE CELL STRUCTURE OF THE SUPERIOR OLIVE IN MAN

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TWO FIGURES

This article includes a description of the cell structure of the superior olive in man and also certain general observations concerning the efferent correlation centers of the dorsal portion of the human medulla, pons, and midbrain (a region for which brevity will necessitate the use of the term brainstem). Nerve cells of the mammalian central nervous system which send impulses towards the peripheral efferent nuclei present a structure characteristic of all efferent cells—a structure which varies according to the functional position of the cell in the efferent pathway (Malone, '13, Anat. Rec., vol. 7, no. 3). In the above article I have pointed out that such premotor cells can be followed throughout the medulla, pons, midbrain, and hypothalamus, and from the last into the globus pallidus of the lenticular nucleus, which is accordingly to be regarded as the efferent portion of the corpus striatum. But subsequent study has convinced me that these premotor cells are much more numerous than had been supposed and that in the older tegmental portion of the human brainstem relatively few afferent cells occur in addition to those in the primary reception nuclei. In other words, cells of the efferent type of structure play a far more important part in local correlation than is at present supposed. The afferent cells of the dorsal portion of the human brainstem are probably not limited to those of the known primary reception nuclei, for doubtless unrecognized reception nuclei exist, and also there is the possibility of the presence within the brainstem of cell bodies of peripheral afferent neurones such as are known in the case of

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system. The fact that the superior olive and the trapezoid nuclei do disperse impulses in so far as they have reflex connections should not obscure the fact that a resumption from these centers of the path to the higher afferent cochlear centers implies the existence of a relay mechanism, a needless break in a definite afferent path. No one would assume that the nature of conduction may not differ according as the dispersion takes place through collaterals or through an interposed center, and with this understanding I repeat my belief that a path is never interrupted except when dispersion occurs. My study of the trapezoid nuclei is as yet not sufficient to permit a conclusive statement, but the cell structure of the superior olive leaves no doubt as to the nature of this center. According to its cell structure it is a typical efferent correlation center, and its cells are such as never send axones to sensory centers such as the higher cochlear centers. Therefore, at least in the superior olive, an impulse from the cochlear reception nuclei once interrupted does not resume its course to the higher cochlear centers.

The specimen here described is from a white male, age forty-five years, who died suddenly; cause of death not determined at autopsy. The brain was removed seventeen hours after death in excellent condition, blood still fluid. Brainstem was hardened in cold 95 per cent alcohol. After several days it was cut into eight pieces, dehydrated in absolute alcohol, cleared in chloroform, and embedded in paraffin. Sections 24μ thick were stained in 1 per cent solution of toluidin blue.

The illustration of the cells of the superior olive of this specimen (fig. 1) renders a detailed description unnecessary, although certain features demand comment. The cells are of medium size, their dimensions being rather uniform when allowance is made for differences due to the manner in which the cells are cut. Their undoubted efferent character is revealed by the relatively large and discrete Nissl granules. The cells in figure 2 are efferent correlation cells from the reticular formation medial to the superior olive, and their structure more nearly approaches that of the peripheral efferent cells, their Nissl granules being almost as large and discrete and their processes almost as definite. In size and

structure these efferent correlation cells of the reticular formation are subject to wide variation; cells occur which can hardly be distinguished from those of the superior olive, others bear a similar relation to the peripheral efferent cells, while the majority of cells are of intermediate types. The cells of the reticular formation shown in figure 2 usually possess more or less yellow pigment as do the peripheral efferent cells; in the illustrations this pigment has been omitted to lessen the expense of reproduction. This yellow pigment is lacking in the cells of the superior olive as well as in those of the preganglionic visceral nuclei. In brains of older individuals it is probable that here also a slight amount of this pigment would be found, but the relative amount in each cell type is approximately constant in the brain of any individual, and accordingly offers a valuable criterion, since it indicates the type of metabolic balance characteristic of each cell type. The cells of the superior olive resemble closely those of the preganglionic visceral nuclei, and at present I am unable to distinguish the latter from this type of efferent correlation cell. Possibly no structural difference should be expected, since both types are really premotor cells, and while the preganglionic cells are related to the visceral system they are by no means unrelated to the somatic system. It appears more in accord with available facts to regard the preganglionic nuclei as efferent correlation nuclei with relations to the efferent visceral system and to the afferent neurones of both systems.

As pointed out by Dolley, the size and structure of each type of cell varies according to the functional state of the individual cell. My observation of various types of nerve cells supports this statement, for within one cell type the individual cells differ as to size, nucleus-plasma relation, and the size, sharpness, and staining of the Nissl granules. The average picture, however, is characteristic of each type. Probably all definite types of efferent nerve cells show relatively little functional variation, as in case of the superior olive. In the efferent correlation cells of the reticular formation the differences are too marked to be explained upon the basis of functional state, and different types of cells corresponding to permanent functional differences must exist.

On the other hand, when the functional unity of an efferent cell group is established the great majority of cells show little variation due to functional state. Examples of such cell groups of uniform function are the large cells of the lateral vestibular nucleus, the peripheral efferent nuclei, and the superior olive; in each of these nuclei differences due to the functional state of individual cells are too slight to cause one to doubt the unity of cell type.



1



2

Fig. 1 Cells of the superior olive in man. Stain toluidin blue. × 600.

Fig. 2 Cells from the reticular formation medial to the superior olive. Stain and magnification same as in figure 1. These cells contain yellow pigment which has been omitted in the illustrations.

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THE SIGNIFICANCE OF THE TERM *HIPPOCAMPUS*

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SIX FIGURES

In describing the coiled tube of a sweat gland as resembling a fairy's intestine, Holmes is said to have indulged in 'useless fancy, transcending the imaginative power of most students—and histologists'; but in contrast with what we are about to consider, this is accurate and prosaic delineation. The flight of fancy which led Arantius, in 1587, to introduce the term *hippocampus* is recorded in what is perhaps the worst anatomical description extant. It has left its readers in doubt whether the elevations of cerebral substance were being compared with fish or beast, and no one could be sure which end was the head. Accordingly the familiar term for which Arantius is responsible is commonly misused and seldom understood, and a brief review of its story should not be altogether unprofitable.

In a scholarly essay,[1] Sudhoff has shown how the four cerebral ventricles, first clearly distinguished by Herophilus and familiar to Erasistratus, were early associated with localized cerebral functions—the fourth with memory, the third with reasoning and reflective thought, the first two, sometimes counted as one, with the receipt of all sensations, being the center both of perception and imagination. With but little variation, this localization was transmitted through the centuries in the writings of theologians and physicians of all schools. The first ventricles were said to be soft and more impressionable; the fourth, harder, and so better fitted to retain a graven record, and moreover colder, to preserve

[1] Sudhoff, W Die Lehre von den Hirnventrikeln. Arch f Gesch d Med, 1913, Bd 7, p 149-222

from that of the fish; but its form, according to Lamer, as judged by the earliest material, had an entirely independent origin. From unknown sources, but uninfluenced by the combinations of the Orient, there appeared in archaic Grecian art, figures of horses terminating as sea-serpents, or as fishes flexible as eels. The first recorded application of the name hippocampus to such a combination is ascribed to Menander; and Scopas (also of the 4th century B.C.) in a lost masterpiece of sculpture which Pliny admires and clumsily praises, is thought to have influenced their artistic evolution. From that time until now, with great variety of fin, web, wings and tail, they have been favorite subjects for poets and artists, and appear on engraved gems and vases, wall-paintings and mosaics, on coins and sarcophagi, and at the present time, especially in fountains.

Albertus Magnus, who to-day might be called Albert the Simple, in a few words seems to give this hippocampus a place in the world's fauna. He writes:

> The horse of the sea is a marine animal, the fore part of which has the form of a horse, but the hind part ends as a fish. It is pugnacious toward many of the marine creatures, and its food is fishes: but man it greatly fears, and can do nothing out of the water, for taken from the water, it straightway dies.[13]

Belon was more critical, as shown in the following passage, from which it appears how closely the river horse, or hippopotamus, and the dolphin were sometimes associated with the hippocampus.

> Very great was the liberty taken by the ancients in their fables! . . . Thus they would have Neptune, distinguished by his trident, drawn through the waters by some hippopotami, as it were, with Nereids going before. According to the artist's fancy, to the great wonderment of the beholder, they so contrived the form of these hippopotami and Nereids, that they seemed of the nature of some hippocampus, rather than hippopotamus. . . . So they are greatly deceived, who place much faith in the vain pictures of the ancients, for in fact there is no hippopotamus with a dolphin's tail or one wound in a circle. . . . But when they wished to show that he reigned by land and sea, they would join together a notable animal of either element—the horse and dolphin—

[13] Albertus Magnus. De animalibus. Mantue, 1479, Liber XXIV; Venetiis, 1495, Liber XXIV, p. 242. Opera omnia, ed. by Borgnet. Paris, 1891, Vol. 12, p. 521.

and the resulting monster because it resembles the form of a marine product (which they call hippocampus) has been given that name by some [14]

Rondeletius ridiculed Belon's picture illustrating this paragraph, as if he had not read the accompanying text

The *Syngnathus hippocampus* of Linnæus as a possible prototype of the mound in the brain, is satisfactorily drawn in figure 2 The shape of the fish happens there to be shown without distracting fins and spines, and in a conventional position In life it rests erect, or suspends itself inverted by its finless prehensile tail, and it does not swim horizontally "It is incapable of flexing the body sideways to any considerable extent," because of its bony armor [15] In color, it has ordinarily no resemblance to the brain, being light brown and speckled, though sometimes yellow, bright red, pale pink, or even nearly white But its most extraordinary feature may perhaps have led Arantius to associate it with the silk-worm In breeding, the female repeatedly approaches the male and by an intromittent organ deposits her eggs, a few at a time, in the abdominal sac with which he is provided, situated at the caudal end of the expanded body In this sac the young develop, nourished by the secretion of its thickened wall, which thus performs some semblance of placental functions Later the young are mechanically expelled through an aperture at the top of the sac The Venetian fishermen, according to Belon, call the hippocampus "faloppa" This apparently refers to the sac, and through a curious coincidence "faloppa" is more commonly used for a "silk-worm cocoon unfinished because of the death of the worm"

Dolphins presumably were not considered by Arantius, though, as already noted, they seem to admit of closer comparison with the cerebral hippocampus This is helped by the incurved shape shown in figure 3, which, however, Belon criticises as being merely an optical effect of the trajectory of their straight bodies when seen leaping from the sea What makes confusion with

[14] Bellonius De aquatilibus Parisis 1553 p 26

[15] These notes are chiefly from citations by Th Gill Proc U S Nat Mus 1905, vol 28 p 805-811

hippocampi possible is that dolphins were frequently shown on the surface of the waves, like the hippocampus in figure 1, with Cupid, Arion, or Nereids as riders. Gesner has referred to the Arion on the dolphin's back with which "Jo. Oporinus, our most industrious and learned printer, marks the books issuing from his press in quick succession, in large numbers, and of the best." Among these was the Fabrica of Vesalius (1543) on the last page of which this printer's device should not be overlooked. The complacent Arion is harping bravely, firmly seated on a dolphin with gill-clefts, which bears its burden with joyless determination. Even though it would have been more appropriate, for several reasons, to have placed a dolphin beneath the lyre of the brain, the text of Arantius hardly justifies this interpretation.

After this review of the introduction of the term hippocampus, and explanation of its setting, it remains to consider the reaction of various anatomists to the situation which Arantius created. Willis altogether ignored it in his "Cerebri Anatome" of 1664, and employed a method of dissection poorly adapted to display the hippocampus. "I unrolled the structures of the brain, as if a sphere had been projected on a plane," he said, but found that the great mass and thickness of the human brain made it unsuitable for unrolling. Taking a sheep's brain, he cut through the ventricles horizontally from behind but did not completely detach this flap, which was then inverted by turning it forward; next, taking the front of the fornix as it lay inverted and behind in this flap, he turned that forward also, and produced a remarkably confusing arrangement which was drawn with extreme inaccuracy as his figure VII. The hippocampus may be recognized, though labeled "margin of the corpus callosum which embraces the medullary stem near the cerebellum." Its relation to the "brachia of the fornix," diminishing into what were later called the fimbriae, is clearly shown.[16]

[16] Willis. Cerebri Anatome, Amstelodami, 1664. Opera omnia, Amstelaedami, 1682. Vicq d'Azyr criticises merely the grill-work texture of the corpus callosum in figure VII; to appreciate the defects of this drawing one should attempt to reproduce it by dissection. A more objectionable modification appears as Tab. V of Willis's, De anima brutorum.

In 1672, Diemerbroeck unostentatiously introduced the term *pedes hippocampi* as a marginal caption in his Anatome. He had described the fornix as possessing one anterior and two posterior pillars, and writes the remarkable statement:

> The posterior crura Hippocrates calls the feet of the hippocampus Riolanus, led by Arantius, thinks that they are extensions of the optic nerves, turned back and upward. . . .[17]

Molinetti, in 1675, described them more fully:

> Two round bodies appear, white beyond belief, composed of the callosal medulla of the brain, each of which accompanies and supports the ventricle of its own side. . . The Latins call them Bombyces, because the size of the bodies, their shape, and the brilliant whiteness wherewith they shine suggest the precious silk-worms . . . The ancients said Hippocampi because the head of the little sea-horse came before the somewhat bifid and sinuous other end. These bodies are nothing else than the posterior crura of the formeate medulla, to which a single third one corresponds anteriorly.[18]

Vieussens in his folio Neurographia of 1685, made no explicit reference to the hippocampi. He thought that the term fornix (that is, vaulted roof) should be transferred to the corpus callosum, *which he recognized as having, not three pillars, but four, namely* "the two roots of the fornix commonly so called, and its two crura," which doubtless are the hippocampi. Propped by this quadruple column, the roof of the brain is kept from "falling in of its own weight."[19] Much more modern in character is a short memoir on the lateral ventricles by J. G. Duvernoi,[20] a Frenchman who by a curious coincidence studied anatomy with J. G. Duverney at Paris, was botanist and professor of medicine

[17] Diemerbroeck Anatome corporis humani Ultrajecti, 1672, p 585 Opera omnia Ultrajecti, 1685, p 350

[18] Molinetti Dissertationes anatomico-pathologicae *"Opus Philosophis utile, Medicis vero necessarium"* Venetiis, 1675, Cap 17, p 185

[19] Vieussens Neurographia universalis Editio nova Lugduni, 1685, p 61 (1st ed , 1684)

[20] Duvernoi, Jo Georg (=Jean Georges Duvernoy) De similibus cerebri Comm acad sci imp petropolitanae Petropoli, 1735 Tomus IV , ad annum 1729, p. 130-135.

Amun Kneph! He had his world-famed temple in the oasis of the Libyan desert, and has left two other mementos in medicine—the gum and sal ammoniac, gathered there from the trees and camels' dung.

Morand, in 1744, rejects both ram's and Ammon's horn, since these objects should taper from their roots to the tip, but those in the brain begin narrow and become clubbed as they diverge; and further, to have horns within horns is needlessly confusing, and the containing horns of the ventricle have prior claim to such designation.[25] So Morand kept the name hippocampus which "Arantius gave and Duvernoi preferred" and proceeded to make known the cock's spur or calcar avis. Bartholin and others had described as a "digital cavity" the posterior horn of the lateral ventricle, and Duvernoi had said that "in this cavity no protuberances were conspicuous." But Morand reports as follows:

In this cavity one sees clearly an outgrowth or protuberance of the medulla, which I shall call *l'ergot* because it resembles perfectly the part of the claw of birds so named, in its outline, shape, and size, with this difference, that without representing its entire thickness, it shows it only in relief. It should be noted that all anatomists have represented the digital cavity as absolutely denuded of any part projecting into it.

Sometimes the posterior cornu is nearly smooth, or provided only with several slight wrinkles suggestive "of folded cloth"; but it may present a large spur such as Morand found, which approaches close to the hippocampus or appears to join it at the convexity of its backward curve. The recognition of the calcar soon affected the terminology of the hippocampus. Thus Haller, who claims for himself the doubtful honor of being first to derive the hippocampi from prolongations of the corpus callosum, delivers his authoritative opinion on these matters in the Elementa of 1762:

Posteriorly it (the corpus callosum) ends in two great swellings like architectural ornaments, which rise up free as half-cylinders; for the rest, they are buried in the medulla of the brain. Each of these swellings becomes split at the posterior end of the ventricle. The shorter part

[25] Morand. Observations anatomiques sur quelques parties du cerveau. Mém. de l'Acad. Roy. de Sci. de l'année 1744. Amsterdam, 1751, p. 430-444.

passes backward and a little inward in the manner of the incurved claw (unguis) of a bird of prey, and fills its end of the ventricle. From it there comes a column, similar in all respects, descending into the horn of the ventricle, the end of which it occupies This longer part unites with the adjacent cerebral medulla interposed between the crura of the fornix; it is compared with a *hippocampus*, and, bent in an arch curved downward and forward, is marked with sulci, not very deep, where it is yoked to the brain; of these I have counted as many as ten. . . .[26] The inferior end of the hippocampus terminates with three, four, or five obtuse parts somewhat like the cloven foot of an animal, but destitute of claws I saw that there were two large upper feet and two small lower ones.[27]

Thus the hippocampus became quadruped. Usually the smaller foot, *pes hippocampi minor*, was recognized in the calcar, as by Gunther and Schreger;[28] and the *pes major* belonged to the hippocampus proper. Malacarne,[29] some years before Haller, had spoken of "the great claw of the foot of the hippocampus," and confusion was rife. Possibly because toes (Zehen, digitationes) were found on both the large and small feet, Mayer considered the name hippocampus no longer appropriate. In his Abhandlung vom Gehirn of 1779, he uses only "pes *hippopotami* major" (or minor).[30] The hippopotamus is listed in the synonymy of the brain by Gunther and Schreger; and Reil, in his Archiv for 1809, employs "Flusspferdefuss" without comment.[31] Burdach ascribes the rejection of hippocampus and the substitution therefor of either pes hippocampi or pes hippopotami as due to a "singular misunderstanding."[32] Hyrtl's inference is that since the fish has

[26] Retzius describes hippocampi with scarcely a trace of such formations Others, he says, end in two rounded mounds with a furrow between; still others have from three to seven elevations, or more, the first of which may be almost cut off by the depth of the adjacent furrow The last ones are generally less well-defined Their varied development is independent of age, sex, or the special development of any known psychic function (Das Menschenhirn Stockholm, 1896, p 67)

[27] Haller Elementa physiologiae corporis humani T 4, Lausannae, 1762, p 34.

[28] Günther Kurzer Entwurf der anatomischen Nervenlehre Düsseldorf, 1789, p 19 Schreger Synonymik der anatomischen Nomenclatur Furth, 1803

[29] Malacarne Encefalotomia Mantoua, 1745, p 25

[30] Mayer Anatomisch-physiologische Abhandlung vom Gehirn, Rückmark, und Ursprung der Nerven Berlin u Leipzig, 1779, p 8

[31] Reil Untersuchungen über den Bau des grossen Gehirns im Menschen Arch. f d Physiol, Bd 9, 1809, p 187

[32] Burdach Vom Baue und Leben des Gehirns Bd 2, Leipzig, 1822, p 372

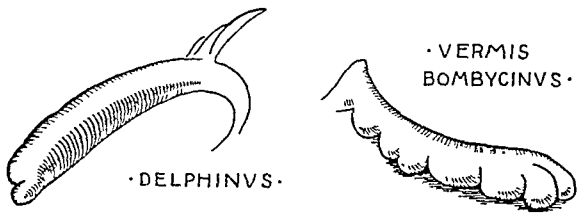
unguis, the German eminentia digitata, the absurd Stiefel or ocrea,[35] and the unjustifiable hippocampus minor or foot of the same. Hippocampus remains, but Ammon's horn goes, together with pes hippocampi (though His places this term at the head of an explanatory paragraph as if he approved it).[36] No longer should there be such mixed metaphors as in Döllinger's figure, where the horn of Ammon is tipped with the foot of the hippocampus.[37] The only regret is that digitationes hippocampi were sanctioned; these hardly need a special name, but they are the *annulations* of the silk-worm or sea-horse.

Only a very young anatomist would propose a new name for a familiar object. The history of these terms is a lesson to that effect. And Arantius erred greatly in giving two names to a single newly discovered structure, even though of a variable shape, not easily described. His successors discarded the more descriptive of these terms for the ambiguous but euphonious hippocampus. Indifferent to its meaning, they found it more distinctive than horns or worms, with which our anatomy is otherwise supplied; and few but their proposers cared for cylindroid swelling, coiled, clubbed or rolled body. How Arantius pictured his sea-horse may remain forever recondite, but with dolphins in mind, hippocampus is more or less appropriate: it may be that some citations we have made show that his description, after all, was not the worst.

[35] Hyrtl (Onomatologia, p. 183) in an effort to explain these names conjectures that the hippocampus has been compared with an Etruscan shoe having a long and upturned toe; but Günther used these names for the calcar avis, and not for the hippocampus as Hyrtl supposed.

[36] His. Die anatomische Nomenclatur. Arch. f. Anat. u. Entw., Supplement-Band, 1895, p. 86 and p. 170.

[37] Dollinger. Beytrage zur Entwicklungsgeschichte des menschlichen Gehirns. Frankfurt, 1814, p. 28, fig. 6.



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THE SUBDIVISIONS OF THE NEURAL FOLDS IN MAN

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SIX FIGURES

Veit and Esch have recently given us the most complete and detailed study of a vertebrate embryo during the period of somite formation that has ever appeared. All the labor and study expended upon it has been well worth while, as human embryos of this period are very rare. The specimen is certainly normal and the preservation above reproach. The embryo has eight somites and belongs to the beginning of the third week, a period which Prof. H. M. Evans and I have been studying for some years. Most of Veit and Esch's findings fit well into the sequence of events as we have interpreted it from our series of embryos. There is, however, a radical disagreement in our interpretations of the nervous system, and in view of the great importance of the Veit embryo to human embryology, it would seem wise to call attention to the matter.

In his first paper based upon this embryo ('18), as well as in the complete description ('22) Veit has adopted a slight modification of the traditional interpretation of the nervous system in young human embryos. This seems to have originated with Kollmann ('89) in his description of the celebrated embryo 'Bulle,' which he had studied simply as a whole mount in balsam. The identification of the regions of the brain was, in the nature of the case, almost wholly subjective. The subsequent writers who have ventured interpretations of the nervous system of embryos younger than 'Bulle' have followed Kollmann more or less closely. They have all made the forebrain relatively enormous and the hindbrain insignificant in size. None of these workers

presence of the fossa in H87, as well as in the younger embryos (e.g., 'Klb' and the Mall embryo no. 391), shows that it is not merely the result of the splitting off of the primordium, as would appear to be the case in the later stages.

Our next stage in the development of the nervous system is represented by Veit's embryo (eight somites), 'DuGa' of Eternod (nine somites), and H392 (U. of C. Coll., eleven somites). The analysis of the second of these is given in figure 3. While I have not studied the sections of this beautiful specimen, I have had the series of accurate and detailed tracings of every section, magnified 200 diameters, made by Professor Evans in the laboratory of Professor Eternod, as well as the latter's descriptions and the Ziegler model. These data, together with the study of the similiar H392, have left few uncertainties as to interpretation. The models and projection reconstructions were stacked from the profile given in figure 5 of Eternod's ('99) paper. In this embryo (fig. 3) the continued growth of the forebrain around the end of the pharynx is associated with the great growth of the midbrain. The rostral end of this region has remained uncertain, as indicated in the figure by the dotted line. The other subdivisions can be recognized in the Ziegler model as well as in our own. The first hindbrain segment of the previous stage has not only increased in length, but has divided into two (*rh.A*$_1$ and *rh.3* in fig. 3), for there are now two segments between midbrain and the otic segment. The hindbrain subdivision A of figures 1 and 2 has split off a neuromere (*rh.3*) caudally, because later stages show that this new segment becomes the first preotic neuromere, i.e., the third rhombomere of the usually recognized series. Crest proliferation has ceased in this segment, but is still present rostrally as far as the forebrain. The cristal and optic primordia are probably continuous here as in other embryos of the same period, but this region is very difficult to interpret because it is cut tangentially. The otic rhombomere of 'DuGa' is typical in form, as may be seen in the Ziegler model, where it can be identified by the fact that the neural folds have closed as far as its caudal end. The first postotic neuromere (*rh.5*) is, as usual, easily recognized and there is an indication of another

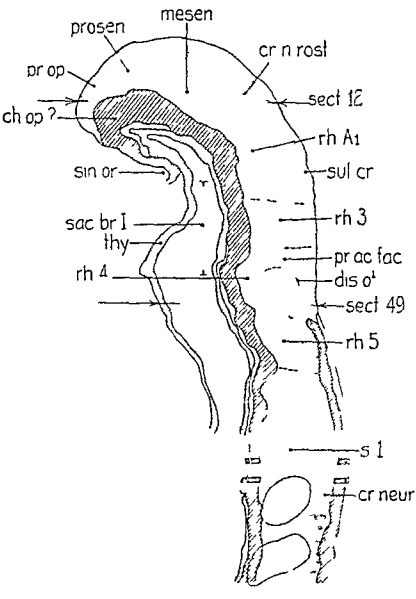


Fig. 3. A projection reconstruction of the head end of Eternod's nine somite embryo 'DuGa' based upon a complete series of tracings made by H. M. Evans. Magnified 200 diameters and reduced one half in reproduction. The neural tube is closed as far forward as the caudal end of the otic segment (*rh 4*). The broken lines at the level of the first somite represent the eight lost sections. The extent of the optic-neural crest primordia is indicated by stippling. *ch op ?*, probably the chiasma ridge, *cr neur*, occipital neural crest, *cr n rost*, rostral division of the neural crest, *disc ot*, otic disc (outlined by dashes), *mesen*, midbrain, *pr ac fac*, acoustico-facial primordium, *pr op*, rostral end of the optic primordium which probably continues caudally to the region of crest proliferation, *prosen*, forebrain, *rh A1*, the remains of the primary first hindbrain segment after the separation of the third definitive rhombomere (*rh 3*), *rh 4* and *5*, the otic and first postotic neuromeres. *sac br I*, the broken line indicates the extent of the first visceral pouch, *sin or* oral sinus, *sul cr*, the clearly cut margin of the stipple indicates the extent of the ventricular cristal sulcus, *s 1*, probable first somite, *thy*, anlage of thyroid. The arrows indicate the levels of the sections of this embryo figured by me in 1922 (figs. 2e and 9b).[2]

[2] Attention may be called here to a misprint in the legend to this figure. The section reproduced as figure 2e is number 21, not 41, of the series.

the rhombomere usually termed the fourth (*rh.4*). All of the other neural segments of this particular two-somite embryo undergo division subsequently. In the series at our disposal the division of the primary segments in general proceeds forward from the hindbrain. Next after the otic, the neuromere just caudal to it (*rh.5*) is cut off, and then the preotic (*rh.3*) makes its appearance. In the meantime the midbrain is growing, but two distinct segments cannot be recognized until after the sixth rhombomere has differentiated. In the sixteen-somite embryo (no. 470) the two mesencephalic segments resemble the hindbrain neuromeres in every respect. From the fourteen-somite stage on there are signs of growth in the first hindbrain segment ($rh.A_1$) and some indications of a subdivision. Low ('08) recognized two rhombomeres here and most students of neuromeres have recognized three preotic rhombomeres. It does not seem evident in the human that the so-called first rhombomere is a complete neural segment. It might be interpreted as merely an enlargement of the alar plate, viz., the early differentiation of the cerebellar anlage.

While it seems probable that in man the differentiation of secondary neuromeres usually begins caudally and proceeds forward, yet this is not necessarily always the case. If we may judge from the conditions in certain lower vertebrates (cf. Locy, '95; B. Smith, '12, et al.), it is possible that there may occasionally be human embryos in which all of the definitive neuromeres can be recognized from early neural-fold stages on. The presence of a definitive neuromere (*rh.4*) at so early a stage as two somites would indicate that the so-called 'primary' and the secondary or definitive neuromeres are expressions of the same fundamental metamerism. B. Smith has expressed a similar idea in saying that certain interneuromeric grooves have a marked tendency to appear earlier than others. Thus we find certain brain segments in most embryos which subsequently undergo subdivision into neuromeres. This phase of the problem richly deserves further study on such favorable material as Cryptobranchus.

SUMMARY

The recognition of certain landmarks furnishes the basis for an analysis of the nervous system in neural fold stages. These are:

1. The otic segment which has been traced through a series of human embryos by virtue of, *a*) its characteristic form; *b*) the behavior of the neural crest which arises from it, and, *c*) its relation to other structures such as the otic plate.

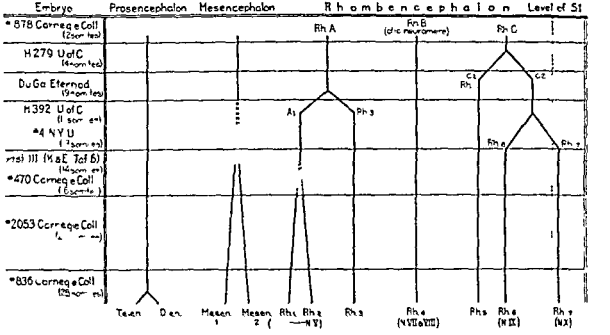


Fig 6 The embryos here included are selected as typical of definite stages in the differentiation of the brain segments In the horizontal columns the segments present in each embryo are shown The bifurcations of the heavy lines indicating the individual segments represent divisions of the original segments This division is preceded in each case by localized growth at that particular level Where this is gradual it is shown by the gradually diverging broken lines

2. The midbrain which is located by the cranial flexure.

3. The first hindbrain segment which, by its peculiar form and the relations of its neural crest, can be directly identified in the older members of the series.

4. The relations of the nervous system to other structures, such as the somites and the pharynx, change gradually and they serve to confirm the interpretation based upon the differentiations of the nervous system.

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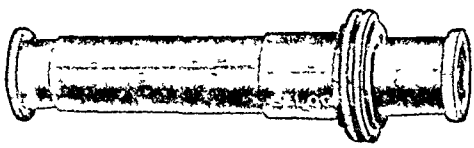
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CONTENTS

BERTIL HANSTRÖM. Further notes on the central nervous system of arachnids: eurypterids, phalangids and trap door spiders. Seven figures ... 249

WILLIAM F ALLEN. Origin and destination of the secondary visceral fibers in the guinea pig. Fifteen figures ... 275

FREDERICK S HAMMETT. Studies of the thyroid apparatus. XII. The effect of thyroparathyroidectomy and parathyroid tomy at 100 days of age on the growth of the brain and spinal cord of male and female albino rats ... 313

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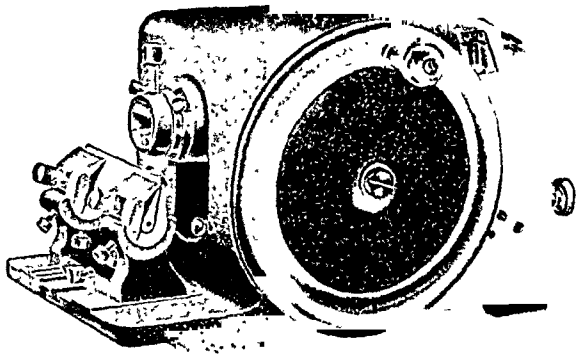
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FURTHER NOTES ON THE CENTRAL NERVOUS SYSTEM OF ARACHNIDS: SCORPIONS, PHALANGIDS, AND TRAP-DOOR SPIDERS

BERTIL HANSTRÖM
Landskrona Gymnasium, Sweden

SEVEN FIGURES

CONTENTS

Introduction . . . 249
Scorpionidea . . . 250
1 General anatomy of the brain . . . 250
2 The cephalothoracic mass . . . 255
3 The free abdominal ganglia . . . 259
Phalangids . . . 263
1 Introduction . . . 263
2 The optic ganglia . . . 263
3 The globuli . . . 268
4 The remaining neurones . . . 270
The Avicularioidea or trap-door spiders . . . 270
General comparison of the optic ganglia . . . 271

INTRODUCTION

This paper is to be regarded as a continuation of my earlier investigations of the central nervous systems of Arachnids ('19, '21). The histological research upon *Phalangium* was done in Sweden some years ago; the examination of the nervous system of scorpions and trap-door spiders was made in 1922 at the Scripps Institution for Biological Research at La Jolla, California.

The Golgi method I have used is the same as described in my papers of 1919, page 53, and 1921, page 3. Both in Phalangium and in Vejovis I have found that the treatment with osmic acid at higher temperature (35°C) is preferable.

In comparing the neurones thus revealed by the Golgi method with those described by other authors, I have thought it most

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Police ('01) has described the fiber tracts in the cephalothoracic mass of scorpions. This description is not sufficiently detailed to permit a comparison with my description of the same nervous mass in araneids ('19). Police speaks of a central column and of ventral columns—the former is certainly the same as my *IV;* they both represent a continuation of the long connectives of the free abdominal ganglia into the cephalothoracic mass. Although the number of abdominal ganglia which participate in the cephalothoracic mass is less in Vejovis (five) than in araneids (ten, according to Pappenheim), I have found the configuration of the more prominent fiber tracts to be the same in both groups (for details see Hanström, '19, p. 24).

The ventral nerves to the pedipalps and the four ambulatory legs and several nerves to the abdomen spring from the cephalothoracic ganglion mass; the abdominal nerves are not united as in the araneids, but proceed posteriorly as small separate nerves. In addition a number of dorsal nerves (ten, according to McClendon) spring from the dorsal regions of the cephalothoracic mass and innervate the muscles of the cephalothorax.

The ganglion cells of the cephalothoracic mass are of three different types: 1) very large, with small nuclei and much cytoplasm; 2) medium-sized, and, 3) small, rich in chromatin, and with a small amount of cytoplasm. The cells lie mostly on the lower surface of the neuropil.

I shall now describe in detail the neurones found in the cephalothoracic mass. I have obtained good preparations of the cephalothoracic mass with the Golgi method, but as it is necessary by this method to section the mass it is difficult to get preparations in which the longer nerve cell processes are uninterrupted. The neurones which I have found in my preparations are illustrated in figure 2.

Motor cells which have their cell-bodies in the ganglion mass and send their axones out in some of the nerves are numbered *1* to *8* in figure 2. They are more or less markedly T-shaped in form; the distal branch is the neurite; the proximal branch sends one or several systems of dendritic branches into the neuropil of the ganglia. According to the extension of the dendritic branches, the motor neurones can be classified into several groups:

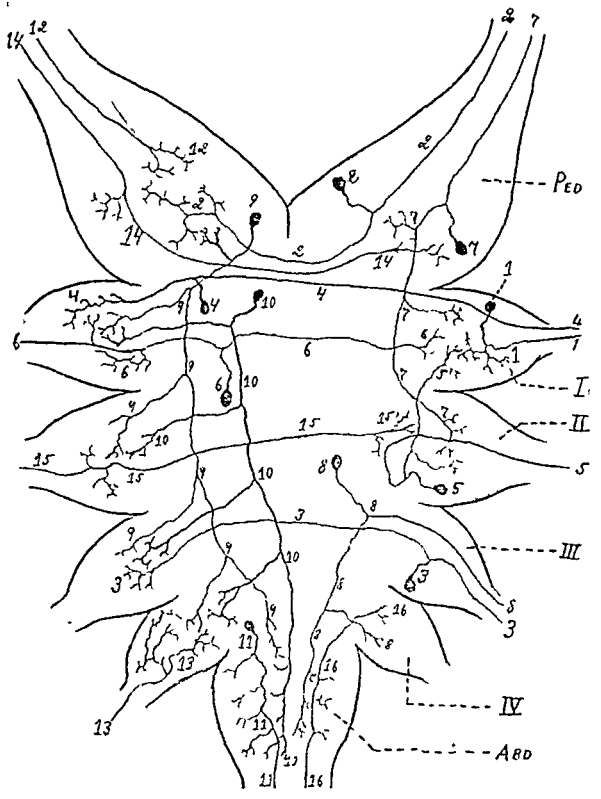


FIG. 2. Horizontal section through the cephalothoracic nerve mass of Vejovis. *I-IV*, ganglia of the legs, *Abd*, five fused preabdominal ganglia, *Ped*, ganglion of the pedipalps.

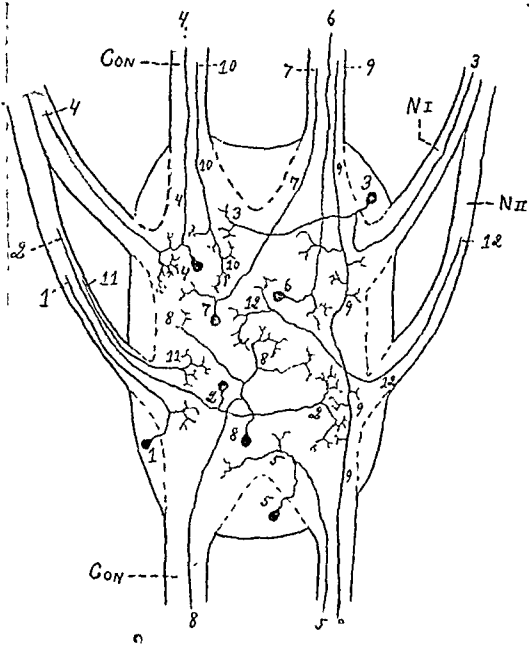
The two members or halves of each ganglionic pair are very closely fused together and are in addition connected by two pairs of commissures. Each pair seems to consist of two dorsal and two ventral commissures, so that in all at least eight transverse fiber tracts are present. The longitudinal connectives between successive ganglia seem also to split up within the ganglion into two dorsal and two ventral fiber tracts on each side.

Two pairs of nerves leave each of the three pre-abdominal ganglia (fig. 3); the anterior pair is connected with the first commissural system, the posterior pair with the second. Both nerves seem to unite shortly beyond the ganglion. I have, however, been able to trace them for only a short distance. I believe these nerves are comparable to the dorsal and ventral nerves which leave each of the components of the cephalothoracic mass. As already described, a smaller dorsal nerve for the muscles of the cephalothorax and a thicker ventral nerve for the pedipalps and ambulatory legs spring from each ganglion of the mass. In the free pre-abdominal ganglia both nerves are of about the same dimensions and leave the ganglion at the same level, but this may be a secondary condition in connection with the disappearance of the abdominal appendages. In the Crustacea, according to Krieger ('80), the nerves of the thoracic ganglia which innervate the legs lie anterior to those which innervate the muscles of the cephalothorax.

The ganglion cells of the free pre-abdominal ganglia are of the same types as in the cephalothoracic mass and are likewise confined almost entirely to the lower surface of the neuropil. The neurones revealed by the Golgi method are represented in figure 3 and will now be described in detail.

Neurones *1* to *4* in figure 3 are motor cells. Of these no. *1* is completely comparable with neurone *1* in figure 2, in the cephalothoracic mass, and neurones *2* and *3*, figure 3, with *2* and *3*, figure 2. Neurone *4*, figure 3, however, which occurs in the first free pre-abdominal ganglion sends a branch (certainly the neurite) out in the first nerve of this ganglion, has dendritic ramifications in the free abdominal ganglia, and sends a branch in the longitudinal connective to the cephalothoracic mass. The whole cell

cannot consequently be followed, but I believe it is connected with a fiber like *16*, figure 2. If this supposition is correct, the neurone in question is comparable with the motor neurones *7* and *8*, figure 2.



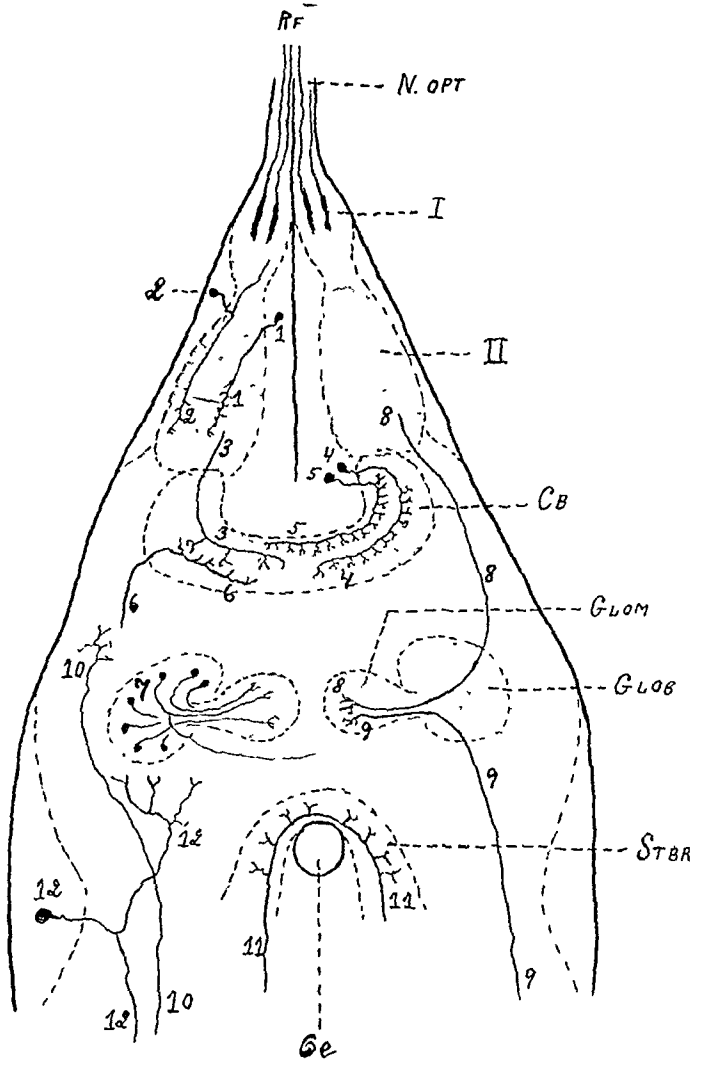


Fig. 4 Schematic figure of the brain of Phalangium opilio, seen from the fr
I and *II*, first and second optic masses; *Cb*, central body; *Glob*, globuli cells; *G*
glomeruli mass connected with the globuli; *N.opt.*, nervus opticus; *Oe*, oesopha
Rf, retinal fibers; *Stbr*, stomodeal bridge. The globuli cells are represented as l
on the anterior side of the brain and the central body is a short distance bel
the lower part of the second optic mass.

I wish to emphasize strongly that there is no ground for distinguishing more than two optic masses in phalangids. The first is clearly homologous with the first optic mass of the median eyes of araneids, as the retinal fibers (figs. 4 and 5, *Rf*) end within it and it is separated from the second by a chiasma which is even indicated in salticids (cf. Hanström, '21, fig. 6), those araneids which have the best-developed median eyes. The whole part of the optic neuropil which lies ventral to the chiasma must be looked upon as a single optic mass because it is morphologically undivided and is surrounded by a continuous layer of ganglion cells. The differences which occur between parts of this mass are no greater than those found between different layers of a highly developed optic mass, such as that of crustaceans or insects.

The second optic mass of phalangids is divisible into a dorsal (fig. 5, *II A*) and a ventral (fig. 5. *II C*) part, which stain deeply with osmic acid or eosin and consist of fibers which course chiefly in a dorso-ventral direction; and a middle layer (fig. 5, *II B*) staining less deeply and composed of fibers running mostly in a horizontal direction.

In the ventral layer (fig. 5, *II C*) of the second optic mass I have found only the T-shaped cells *8* to *10* already described and the terminations *11* and *12* of fibers which come from the protocerebrum.

Connections between the second optic mass and other parts of the brain are represented by fibers *3* and *8* in figure 4. The former gives confirmatory evidence by means of the Golgi method of those connections between the second optic mass and the central body which are easily observable in preparations stained by ordinary methods. Fiber *8*, figure 4, which is the same as fiber *8*, figure 6, and fiber *7*, figure 6, represent connections between the optic ganglia and the globuli, also found by Kenyon in insects and by me in araneids and crustaceans.

As the eyes of phalangids are homologous with the medial eyes of araneids, a comparison of the optic ganglia of the two groups is possible through my investigation of the araneids (Hanström, '21, p. 15, fig. 6, and p. 36). The chiasma cells *6* to *8* in araneids are then quite like the neurones *1* to *3*, figure 5, in phalangids, and fiber *10* in Marptusa seems to have the same relations to the chiasma cells as fibers *6* and *7*, figure 5, have in phalangids.

3. The globuli

The globuli of Phalangium, contrary to the condition in Gonyleptis (Holmgren, '16), are quite insignificant bodies, but the deeply staining properties of their small cells make them conspicuous parts of the ganglion cell layer.

The chief cells of the globuli are small cells, which stain very deeply with iron haematoxylin. I have also obtained several of these cells impregnated with silver in Golgi preparations (fig. 4, *7*, and fig. 6, *1* to *5*). The fiber bundles join to form a kind of stalk which is connected with the glomeruli mass (fig. 6, *Glom.*). Some of the fibers (fig. 6, *4*, *5*) do not seem to split up until they reach the small glomeruli masses of which the big mass (*Glom.*) is composed. In these small glomeruli masses the fibers form dense nets of fine ramifications. The small cells may be regarded as local cells of the globuli. Other globuli cells (fig. 6, *1* to *3*) send a long fiber into the commissure of the globuli (fig.

6, *Pbr.*), while shorter branches pass to the glomeruli. These latter cells are comparable with the globuli cells which I described in 1921 in salticids and lycosids ('21, figs. 3 and 7) as participating in a commissure. Their structure—a dendritic branch sent into the glomeruli and a long undivided neurite—is very similar to that of the globuli cells of the insects, described by Kenyon ('96). The termination of the neurite in phalangids is, however, certainly branched (fig. 6, *6*) while according to the account of

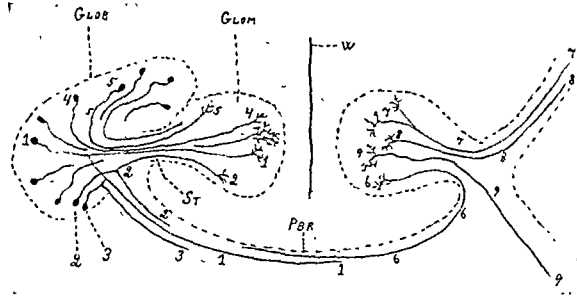


Fig. 6 Cross-section through the globuli of Phalangium. The left half is represented as anterior to the right half. *Glob*, globuli cells; *Glom*, glomeruli mass; *Pbr*, protocerebral bridge or commissure between the globuli; *St*, stalk of the globuli cells; *W*, wall of connective tissue between the two halves of the brain.

Kenyon, the globuli cells of the bee end without branching, and further do not participate in a commissure.

The commissure in phalangids is not very prominent; it is not, as in other arachnids (scorpions, pedipalps, araneids), of glomerular structure, but must for comparative reasons be regarded as homologous with the protocerebral bridge of other arthropods.

The glomeruli masses connected with the globuli cells reveal their function as associative centers by their connections with the optic ganglia (fig. 4, *8;* fig. 6, 7, *8*) and with the suboesophageal mass (fig. 4, *9;* fig. 6, *9*).

The lateral and medial eye nerves of arachnids pass into a portion of the brain which is designated the optic lobe. The optic lobe is composed of several optic 'ganglia,' each of which consists of a central mass of neuropil called the optic mass surrounded by a layer of ganglion cells which are frequently of the small, chromatin-rich type described in this paper.

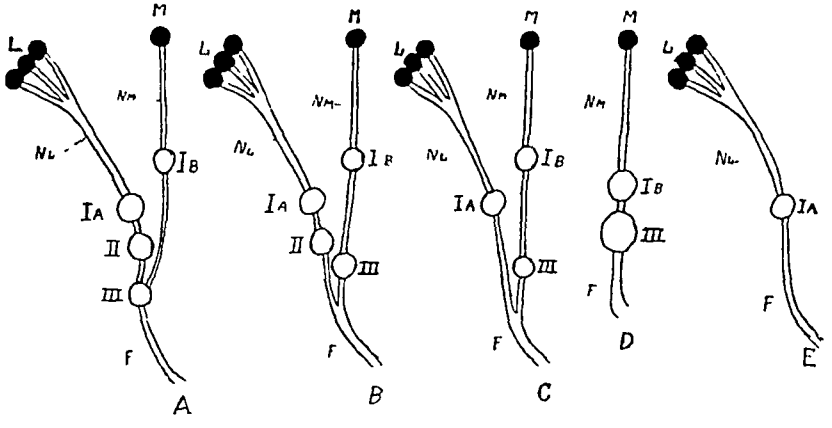


Fig 7 Schematic figure of the eyes and optic masses in arachnids. A, scorpions; B, lycosid, thomosid, and salticid araneids; C, web-spinning araneids, pedipalps, and solpugids; D, phalangids; E, chernetids and acarids *F*, fibers going towards the central body; *L*, lateral eyes; *M*, medial eyes; *Nl* and *Nm*, nervus opticus lateralis and medialis; *IA*, *IB*, *II*, *III*, optic masses No consideration is taken in the figure of the number of lateral eyes, which is very variable among the different groups of arachnids.

The scorpions (fig. 7, A), as already stated, have three optic masses in the lateral eye nerve (*IA*, *II*, *III*) and two in the median nerve (*IB*, *III*), but the last of these organs (*III*) is common to both nerves. The optic mass *III* is rather large in this group of arachnids, but the ganglion cells which partially cover it are not of the small, chromatin-rich type which characterize the other three optic masses (*IA*, *IB*, *II*).

In the lycosid, thomisid, and salticid araneids (fig. 7 B) there are present in the lateral eye nerve only the first two optic masses of scorpions (*IA* and *II*). The third optic mass (*III*) seems to

be connected only with the medial eye nerve, is very small, and has no connections with the small, chromatin-rich ganglion cells. The medial eye nerve is then provided with the same two optic masses as in scorpions, namely, *IB* and *III*.

In the web-spinning spiders (families Epeiridae, Theridiidae, Agalenidae, Drassidae, Dictynidae, Dysderidae) the second optic mass of the lateral eye nerve of scorpions has been lost and only the first (fig. 7C, *IA*) has been retained. The number and structure of the optic ganglia of the medial nerve persist unchanged (*IB* and *III*). The optic ganglia of the pedipalps and solpugids are the same as in these spiders.

The phalangids (fig. 7D) completely lack the lateral eyes and the optic ganglia belonging to them. The two optic masses of the medial eyes (*IB* and *III*) are present and reach a high degree of differentiation.

In contrast to the phalangids the chernetidans and acarids (fig. 7E) have lost the medial eyes and their optic masses. Like the web-spinning spiders, the pedipalps and the solpugids, they retain only the first optic mass of the lateral eye nerve (*IA*).

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LITERATURE

Considerable evidence has accumulated suggesting the presence of visceral fibers, other than taste, in the forebrain and midbrain. There is general agreement in attributing respiratory functions to the nucleus commissuralis, but there is considerable difference of opinion as to the existence and location of definite heat and respiratory centers in higher areas.

As early as 1884, Ott claimed the existence of certain heat centers about the human corpus striatum. A year later he found that injuries to the anterior part of the thalamus resulted in a rise in temperature, and in 1889, these heat centers were extended to include an area about the Rolandic fissure. Richet, White, Tangl and Sinelnikow have also described rises in temperature in various animals, resulting from lesions in the region of the thalamus and corpus striatum. Howell and Austin found that stimulating the sigmoid gyrus in dogs gave a constant vaso-motor effect, and stimulating the caudate nucleus produced a marked rise in blood pressure with inhibition of respiratory movements. Prince and Hahn found a heat center in cats and rabbits, 5 mm. lateral of the sagittal suture and 5 mm. cephalad of the coronal suture, by stimulating this area with heat, while stimulating a similar region 5 mm. caudad of the coronal suture did not produce a corresponding thermal change. A number of other papers quoted by Sachs ('11) ascribe heat and respiratory centers to the thalamus. Mosso on the other hand attributed this rise in temperature to hemorrhages, excitement, and muscular contractions. Miss Moore also claims that the corpora striata of birds and rabbits are not essential for the maintenance of constant body temperature and doubts the existence of heat centers in the brain.

Sachs ('11) after electrical stimulation of many different parts of the thalamus and corpus striatum in some 60 cats, arrived at the conclusion, that "the optic thalamus contains no centers, which upon direct stimulation, produced changes in temperature." He maintains that the portion of the thalamus which causes changes of blood pressure and respiration are in the regions of the large afferent pathways, and since the results are very similar to those obtained from severing an afferent nerve, he assumes

that there are no circulatory and respiratory centers in the thalamus. Sachs found, however, that stimulating the nucleus lentiformis inhibits respiration.

Rogers observed that pigeons could maintain a normal temperature when placed in a cage at a temperature of from 4° to 38°C., and that decerebrated pigeons could also maintain a normal temperature when placed in a temperature of from 5° to 38°C. In contrast, when the optic thalamus of decerebrated birds was almost completely cauterized, the temperature regulating mechanism was so affected that the temperature of the bird was largely determined by its surroundings. In these pigeons the temperature was lowered to 19° or raised to 46°C., by varying the temperature from 10° to 38°C.

Apparently the reactions of the thalamus of pigeons are very different from those of mammals, and it is possible that there is as much difference in the functions of the thalamus of birds and mammals as there is between the functions of the colliculus superior of the lower vertebrates and mammals.

Lewandowsky, Brown, Treven, Miss Coombs, and others have indicated the possibility of a respiratory center or at least a respiratory relay station in the midbrain. Brown upon stimulating the colliculus superior in the region of the tractus tectospinalis obtained a rapid panting movement of the abdominal respiratory muscles of the monkey, which stopped when the stimulation stopped. Miss Coombs found that sectioning the colliculus inferior in the cat resulted in a deeper and slower respiration. Also severing the dorsal roots of the thoracic and cervical nerves produced a similar diminution of the costal respiration. A section of the colliculus inferior subsequent to sectioning the dorsal roots of the cervical and thoracic spinal nerves produced a greater effect on the costal respiration than severing the spinal roots alone; while the reverse order showed no more change than severing the colliculus inferior alone.

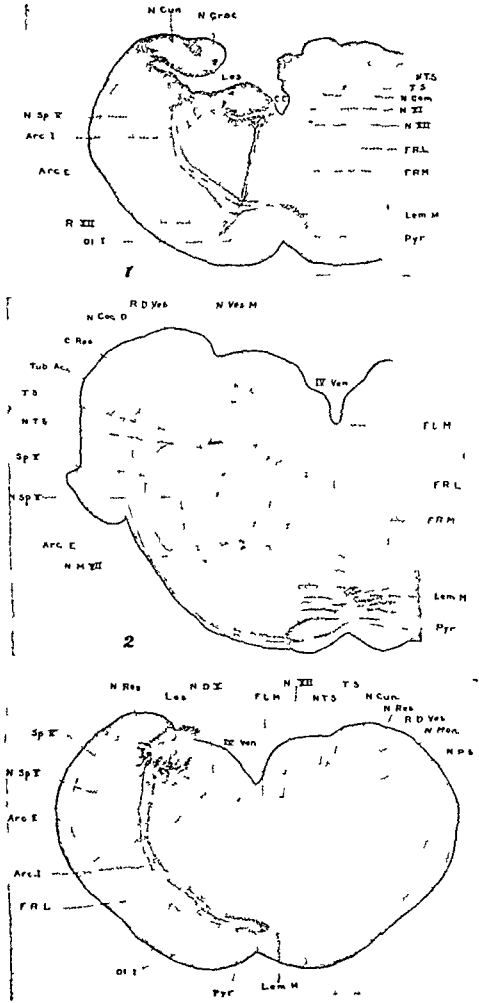
Van Gehuchten states in his textbook (pp. 853-5) that the Marchi method does not reveal any bulbo-thalamic or bulbo-cortical fibers arising from lesions in the region of the tractus solitarius. He is of the opinion that there must be a gustatory

N.Den., nucleus dentatus
N.D.X., nucleus motorius dorsalis nervi vagi
N.Emb., nucleus emboliformis
N.F., nucleus fastigii or tecti
N.Glob., nucleus globosus
N.Grac., nucleus fasciculi gracilis
N.Lat.T., nucleus lateralis thalami
N.L.F.R., nucleus lateralis formatio reticularis
N.L.Lem., nucleus lemnisci lateralis
N.Mon., nucleus Monakow of Winkler's descriptions
N.M.VII, nucleus motorius nervi facialis
Nod., nodulus
N.P.D., nucleus pontis dorsalis
N.P.S., *nucleus parasolitarius*
N.P.V., nucleus pontis ventralis
N.Res., nucleus proprius corporis restiformis
N.R.Mes.V, nucleus of the radix mesencephalicus nervi trigemini
N.Rub., nucleus ruber
N.Sp.V, nucleus tractus spinalis nervi trigemini
N.T.S., nucleus tractus solitarii
N.V.Br.C., nucleus ventralis brachii conjunctivi
N.Ven.T., nucleus ventralis thalami
N.Ves.M., nucleus nervi vestibularis medialis (Schwalbe)
N.Ves.Sp., nucleus nervi vestobularis spinalis
N.V.F.R., nucleus ventralis formatio reticularis
N.III, nucleus nervi oculomotorii
N.XI, nucleus nervi accessorii or caudal continuation of the nucleus motorius dorsalis nervi vagi
N.XII, nucleus nervi hypoglossi
Ol.I., nucleus olivaris inferior
Parafl., paraflocculus
Ped.Cer., pedunculus cerebri
Ped.C.M., pedunculus corporis mamillaris
Pyr., pyramis or tractus cortico-spinalis
R.D.Ves., radix descendens nervi vestibularis and tractus arcuatus (Russell)
R.M.VII, radix motorius nervi facialis (pars secunda)
R.M.X, radix motorius nervi vagi
R.Subt., regio subthalamica or nucleus hypothalamicus
R.Ves., *radix nervi vestibularis*
R.III, radix nervi oculomotorii
R.V, radix nervi trigemini
R.IX, radix nervi glossopharyngei
R.XII, radix nervi hypoglossi
Sp.C.D., tractus spino-cerebellaris dorsalis
Sp.C.D., tractus spino-cerebellaris dorsalis
Sp.C.V., tractus spino-cerebellaris ventralis
Sp.V., tractus or radix spinalis nervi trigemini
St.Ac., striae acusticae or medullares
T.Hab.Ped., tractus habenulo-pedunculares
T.S., tractus or fasciculus solitarius
Tub.Ac., tuberculum acusticum
Ves.Crb., fibrae vestibulae cerebelli
IV.Ven., ventriculus quartus

Fig. 1 Transverse section from *Marchi* series No. 99, showing extent of the lesion through the left nucleus tractus solitarii and nucleus commissuralis, together with resultant degeneration. This figure is from approximately the same level as figure 18 of the previous paper. × 8.3.

Fig. 2 Left half of a more cephalic section from the same series as figure 1, at the level of the tuberculum acusticum. × 8.3.

Fig. 3 Transverse section from Marchi series 140, showing lesion through center of the general visceral division of the nucleus tractus solitarii, and resultant degeneration. This section is the sixth section above the union of the ventriculus quartus with the canalis centralis and at approximately the same level as figure 16 of the previous paper. × 8 3.


N Cun
N Grac
Lea
NTS
T S
N Com
N XI
N III
FRL
FRM
N Sp V
Arc I
Arc E
R XII
Ol I
Lem M
Pyr
1
R D Ves
N Ves M
N Coc D
C Res
Tub Ac
T S
N T S
IV Ven
FLM
Sp V
FRL
N Sp V
FRM
Arc E
N M VII
Lem M
Pyr
2
N Res
N D X
Lea
N XII
T S
FLM
NTS
N Cun.
N Res
R D Ves
N Mon.
N P S
Sp V
IV Ven
N Sp V
Arc E
Arc I
FRL
Ol I
Pyr
Lem M

clear through the medulla, a little to the left of the median line, at the level of the entrance of the nervous facialis, and finally drawing the needle caudad to the level of the entrance of the last sensory root of the vagus. A study of these two lesions in series 116 reveals that all of the fibers going from the nucleus tractus solitarii to the opposite lemniscus would be severed. Consequently if the secondary visceral fibers enter the opposite lemniscus medialis as von Monakow maintains, and they are medullated, their distribution can be followed in this series.

An examination of a section (fig. 7) of series 116 at the level of the center of the gustatory division of the nucleus tractus solitarii, clearly shows the narrow cephalic lesion (*Les.*) severing the left formatio reticularis. As a direct result of this lesion, degenerated fibrae arcuatae dorsales (*Arc.D.*) appear on both sides of the incision. Since these fibers cannot be traced beyond the descending vestibular root fibers, since they pass through the nuclei of the solitary tracts, and since this area is cephalad of the dorsal muscle sense nuclei and caudal of the tuberculum acusticum; it is probable that the fibrae arcuatae dorsales are vestibular fibers at this level. Furthermore this lesion severs some fibers designated as fibrae arcuatae internae (*Arc.I.*), which apparently go to the lemniscus medialis (*Lem.M.*) of the opposite side. These fibers may be gustatory fibers from the nucleus tractus solitarii or they may be general cutaneous fibers from the nucleus tractus spinalis nervi trigemini or both. Fibrae arcuatae internae were also observed in several neighboring sections, but in other neighboring sections they were either absent or mixed with the formatio reticularis. The more extensive caudal lesion undoubtedly accounts for most of the degenerated fibers found in the corpora restiformia, in the fasciculi longitudinales mediales, and in the left lemniscus medialis.

Distribution of the degenerated lemniscus medialis fibers

Before describing the distribution of the lemniscus medialis in series 116 it seems advisable to record briefly some of the earlier work on this tract. It can be stated at the outset that considerable disagreement exists concerning the distribution of the lem-

niscus medialis fibers. For example, direct fibers have been described going to the cerebellum and cerebral cortex. Bruce ('93), Rothmann, and Wallenberg think that lemniscus medialis fibers supply the colliculus inferior; while Ferrier and Turner traced a few fibers to the colliculus superior, and Wallenberg followed a few fibers to the corpus mamillare and to the hypothalamus. Mott ('98) clearly states that all fillet fibers end in the optic thalamus and none continue to the cerebral cortex. Van Gehuchten followed lemniscus medialis fibers to the nucleus lateralis of the thalamus, and claims that no direct fibers go to the cerebellum, corpora quadrigemina, or to the cerebral cortex. Probst traced the lemniscus chiefly to the ventral thalamic nucleus.

The lemniscus medialis (fig. 8B, *Lem.M.*) is situated immediately dorsal of the pedunculus cerebri (*Ped.Cer.*) and lateral to the ganglion interpedunculare (*G.Intp.*) at the level of the colliculus inferior in series 116. There is no evidence of degenerated fibers supplying this ganglion or the colliculus inferior. Degenerated lemniscus fibers, however, extend out laterally, nearly to the outer margin of the section. This section also shows degenerated fibers in the fasciculi longitudinales mediales, but they were accounted for through the direct caudal destruction of these tracts.

A section through the lemniscus medialis (fig. 8A, *Lem.M.*) at the level of the colliculus superior and the caudal end of the corpora mamillaria demonstrates this tract as being spread out, ventro-laterally, directly beneath the nucleus ruber and brachium conjunctivum (*N.Rub.* and *Br.C.*). It lacks considerably the width it possessed in figure 8B and its fibers are much more condensed. In this and adjacent sections there are apparently a few more degenerated fibers in the ventral part of the nucleus ruber, in the ventral formatio reticularis, and in the regio subthalamica or nucleus hypothalamicus (*R.Subt.*) than are present in areas not supplied by lemniscus fibers. There are apparently more degenerated fibers in the nucleus ruber than in the hypothalamic region and more in the cephalic end of the nucleus than in the caudal end. The number of these degenerated fibers is not striking in any place, and nothing resembling a tract can be traced to these areas. In all of my series where the nucleus

and *N.Glob.*); a second or smaller mass of degenerated fibers is likewise passing caudally, above and between the left and right nucleus fastigii (*N.F.*); while other degenerated fibers are crossing to the opposite side in the commissura cerebelli anterior (*C.Ant.*). These degenerated fibers pursue a course parallel to many normal fibers, which will be shown to be, in part, tractus spino-cerebellaris dorsalis fibers. A section taken from below the last cerebellar peduncle and lingula, demonstrates that many of the degenerated fibers in the lateral tract (*M.S.F.*) have acquired a more ventral position between the nucleus globosus (or the combined intermediate nuclei) and the left nucleus fastigii. The median group of degenerated fibers has increased in number and has likewise attained a more ventral position, some degenerated fibers appearing even ventrally to the nucleus fastigii. Also at this level there are more than the normal number of degenerated fibers in the left nucleus fastigii, but the other more lateral cerebellar nuclei contain no more than the normal number of degenerated fibers. The degenerated fibers in the right or opposite corpus restiforme, although much fewer in number, have apparently a similar relationship to the right cerebellar nuclei.

Most of the series, where the lesion involved the cephalic or gustatory portion of the nucleus tractus solitarii, could not be used for this phase of the problem, on account of direct injury to one or more of the basal cerebellar nuclei. In series 138, where the lesion destroyed the caudal part of the gustatory division of the nucleus tractus solitarii in addition to a large part of the general visceral division of this nucleus, there is identically the same relationship of degenerated corpus restiforme fibers to the basal cerebellar nuclei as was shown in series 117 described above. Also in series 116, where the lesion destroyed all of the general visceral division of the nucleus tractus solitarii and all of the fibrae arcuatae dorsales going to the right or opposite corpus restiforme, there is the same relationship of degenerated corpus restiforme fibers to the basal cerebellar nuclei as was described above for series 117. Likewise in series 164 and other series, where the lesion involves only the dorsal muscle sense nuclei of the medulla, the degenerated fibers in the corpus restiforme have

a distribution identical with those described above for series 117. Finally, the distribution and relationship of the degenerated corpus restiforme fibers in the cerebellum of series 117 and the above mentioned series, are identical with the left tractus spino-cerebellaris dorsalis fibers, as shown by series 113 where this tract was severed in the upper cervical region, and by series 93 where this tract was severed in the lumbar region.

The literature discloses some differences concerning the distribution of the tractus spino-cerebellaris dorsalis. Mott does not mention the relation of this tract to the cerebellar nuclei. Collier and Buzzard found tractus spino-cerebellaris dorsalis fibers supplying the nucleus dentatus in man. Bruce ('98), and MacNalty and Horsley did not describe any tractus spino-cerebellaris dorsalis going to the nucleus dentatus, but the latter found collaterals from the tractus spino-cerebellaris ventralis supplying the nucleus fastigii. Ingvar states that a small part of the tractus spino-cerebellaris dorsalis fibers appear to end in the cephalic cerebellar nuclei, especially in the nucleus tecti (fastigii).

In the way of a summary for this section it can be stated that series 117 and the following series described above, show degenerated corpus restiforme fibers curving over the cephalic surface of the nucleus dentatus. These fibers pass caudally, in lateral and median bundles, situated above and between the three medial cerebellar nuclei, and they end caudally in the adjacent cortex. There is always more than the normal number of degenerated fibers in the nucleus fastigii, but whether these fibers terminate in this nucleus or continue through it to end in the adjoining cortex was not determined. No more than the normal number of degenerated fibers is found in the nucleus dentatus, emboliformis, et globosus, but on the other hand it must be admitted that the cells of these nuclei would not have to possess very long dendrites to form a synapse with these corpus restiforme fibers. The general indication is, however, that the degenerated fibers in the corpus restiforme of these series are for the most part, if not entirely, muscle sense fibers passing to the cerebellar cortex.

rhage occurred it was stopped with bone wax, prepared after a formula given in a previous paper. The instrument used in making this lesion consisted of a small chisel, having a blade about one third of the width of the brain stem. The incision was made through the left cerebral hemisphere, directly in front of the sinus transversus, and extending from the median line laterally. The chisel was at first pointed caudo-ventrad; then after bending outward to avoid cutting the fasciculus longitudinalis medialis, it was brought back to the median line and finally carried deep enough to completely sever the left lemniscus medialis and pedunculus cerebri, without crossing to the opposite side and without severing the main ventral arteries. The two temporal muscles were sewed together with fine sterile thread so as to cover the hole in the skull, and finally the skin incision was closed with coarse sterile thread and coated with iodine.

Since the cells of the nucleus tractus solitarii are relatively small, the animals were killed 6 to 8 days after the operation. If they were permitted to live much longer, many of these cells would undergo complete degeneration and become obliterated.

After many failures, some of which resulted in the severance of the fasciculus longitudinalis medialis, the destruction of parts of both lemnisci, or the failure to completely sever the left lemniscus medialis, series 177 was obtained, which demonstrated a very satisfactory lesion. This lesion (fig. 9, *Les.*) passed to the side of the left fasciculus longitudinalis medialis (*F.L.M.*), completely severed the left lemniscus medialis and pedunculus cerebri, but apparently did not injure the opposite lemniscus or pedunculus cerebri (*Lem.M.* and *Ped.Cer.*). Unfortunately the sections of this series were inverted so that the lesion appears on the right side instead of the left.

Figure 10 illustrates a section through the extreme caudal end of the general visceral division[2] of the right or opposite nucleus tractus solitarii and nucleus commissuralis from series 177. This section is approximately at the same level as figure 18 of the previous paper, which shows many degenerated fibers ending, medially, in the nucleus commissuralis, and a few, laterally, in

[2] See footnote 1, p. 283.

the nucleus tractus solitarii It is obvious from figure 10 that the large cells in the nucleus tractus solitarii (*N T S*) are perfectly normal in every respect Likewise the larger cells of the nucleus

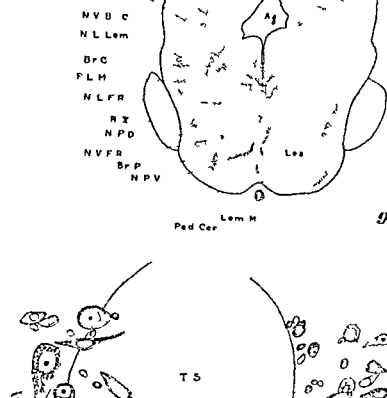


Fig 9 Taken through the center of the lesion from Nissl series 177 The lesion has severed the left lemniscus medialis without injuring the opposite lemniscus or either fasciculus longitudinalis medialis or the cerebellum In this series the sections were inverted so that the lesion appears on the right side instead of the left $\times 6.6$

Fig 10 Section showing normal cells in the right nucleus tractus solitarii and nucleus commissuralis (caudal portion of the general visceral division of this nucleus) from the same series as figure 9 and at approximately the same level as figure 18 of the previous paper $\times 127$

commissuralis (*N Com*) have sharply defined and centrally placed nuclei with perfectly normal and sharply differentiated Nissl substance The opposite nucleus tractus solitarii and

the smaller cells show more advanced stages of atrophy. Adjacent sections through this nucleus present a similar picture; while sections through the opposite nucleus tractus solitarii exhibit, for the most part, perfectly normal cells. A section through the middle portion of the gustatory division of the right nucleus tractus solitarii (fig. 13) also discloses cells in all stages of chromatolysis. An early stage is illustrated by (a), a medium stage by (b) and an advanced stage by (c). Many of these cells are representatives of an early stage of chromatolysis, portraying a diffuse staining of the protoplasm and an eccentric position of the nucleus. One cell (n) is apparently normal. Adjacent sections also show a similar chromatolysis of the cells of this nucleus. The cells in the opposite or left nucleus tractus solitarii of this section (fig. 14A) are perfectly normal, with the possible exception of (d), which gives evidence of some disintegration. In the next section of the left nucleus (fig. 14B) the cells are all normal. In Nissl series it is impossible to locate with certainty the extreme cephalic end of the nucleus tractus solitarii; so that nothing definite can be stated for the extreme cephalic end of the gustatory division of this nucleus. No chromatolytic cells, however, were found in this general region in series 177.

It is apparent from this experiment (177), that severing the left lemniscus medialis in the midbrain region, without injuring the fasciculi longitudinales mediales, opposite lemniscus, or cerebellum, causes chromatolysis of most of the cells throughout the entire gustatory division of the opposite nucleus tractus solitarii, excepting possibly a small area in the extreme cephalic end of this nucleus. It also produces chromatolysis of many of the cells of the cephalic half of the general visceral division of the opposite or right nucleus tractus solitarii; but does not bring about any chromatolysis of the cells of the caudal or commissural half of the general visceral division of the right nucleus tractus solitarii. The caudal half of the general visceral division of this nucleus, which is composed largely of the nucleus commissuralis, comprises three fourths of the bulk of the general visceral division of the nucleus tractus solitarii. It might be mentioned in this connection that the 33d cm. plane, or the junction of the ventric-

ulus quartus with the canalis centralis in figure 1 of the previous paper, indicates a more or less clear dividing point of the tractus solitarius fibers supplying the sensory nuclei, which corresponds very well to the line of separation between the two halves of the general visceral division of the nucleus tractus solitarii described above.

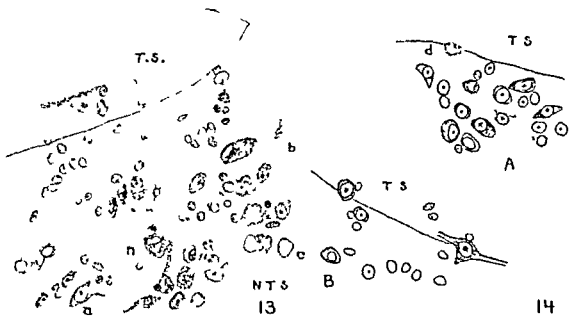


Fig 13 Chromatolytic cells from the center of the gustatory division of the right nucleus tractus solitarii from the same series as figure 9 and from approximately the same level as figures 6 and 7 of the previous paper × 191

Fig 14A Normal cells in the opposite nucleus tractus solitarii of the same section as figure 13 and on the same side as the lesion of the lemniscus × 191

Fig 14B Normal cell from the same nucleus as 14A, but from the next section × 191

The previous Marchi and Nissl experiments, together with the fact that it is very doubtful if any ascending fasciculis longitudinalis medialis fibers reach the diencephalon, are sufficient to exclude this tract from the possibility of conveying secondary visceral fibers to the thalamus. As further evidence that this tract does not contain secondary visceral fibers, series 168 is introduced. In this series the lesion severed both fasciculi longitudinales mediales without injuring the lemnisci, with the result that there are no more than the normal number of chromatolytic cells in either nucleus tractus solitarii or in the nucleus commissuralis.

with them; and in a third series of experiments the spinal cerebellar tracts were severed in the upper cervical region. The results were identical in all series, namely, the cells of the basal cerebellar nuclei of both sides are perfectly normal.

SUMMARY AND GENERAL CONSIDERATIONS

Marchi experiments.—On account of the close relationship of the nucleus tractus solitarii to the fibrae arcuatae internae from the dorsal muscle sense nuclei of the medulla and to the vestibular, secondary trigeminal, and auditory fibers it is impossible in the Marchi experiments to exclude the possibility of severing some of the above fibers in destroying the nucleus tractus solitarii, no matter how restricted the lesion may be.

Lesions of the caudal part of the nucleus tractus solitarii and nucleus commissuralis always produce degenerated fibrae arcuatae internae going to the opposite lemniscus medialis. These are largely, if not entirely, muscle sense fibers from the nucleus fasciculi gracilis. Apparently, lesions that are confined to the nucleus commissuralis do not result in the degeneration of any ascending fibers. Lesions through the cephalic half of the general visceral division of the nucleus tractus solitarii and all but the extreme cephalic portion of the gustatory division of the nucleus tractus solitarii bring about degeneration of fibers in the opposite lemniscus medialis and in the corpus restiforme of the same and opposite sides, especially in the former.

As a result of tracing these degenerated corpus restiforme fibers into the cerebellum, none are visible in the nucleus dentatus, emboliformis, and globosus; some are present in the nucleus fastigii, but they may only penetrate this nucleus to reach the cortex. For the most part these fibers pass, caudally, above and between the cerebellar nuclei to the more caudal cortex. They have a course identical with the degenerated tractus-spino-cerebellaris dorsalis fibers, resulting from lesions of this tract in the lumbar and in the upper cervical regions of the spinal cord. Probably these degenerated fibers are muscle sense fibers destined to go to the cortex of the cerebellum.

The Marchi series in which all of the fibrae arcuatae internae going to the opposite lemniscus were cut, and, in fact, all of the more restricted lesions of the nucleus tractus solitarii that produced degenerated fibers in the opposite lemniscus prove that, if there are any medullated general visceral and gustatory fibers of the second order in the lemniscus medialis, they are distributed mainly to the nucleus ventralis et lateralis thalami. It was noted that there are apparently a few degenerated lemniscus fibers in the formatio reticularis surrounding the thalamus, in the regio subthalamica and in the nucleus ruber; but none are present in the ganglion interpedunculare, corpora mamillaria or tuber cinereum. An identical distribution of lemniscus medialis fibers was also recorded for several series where the lesion was confined to the nucleus fasciculi cuneati et gracilis.

It is apparent that these Marchi series would not account for any non-medullated fibers that might go to the diencephalon or to the basal nuclei of the cerebellum.

Chromatolysis experiments.—A Nissl series in which the left lemniscus medialis was severed in the midbrain region without injuring the corresponding fasciculus longitudinalis medialis, opposite lemniscus, or cerebellum demonstrates chromatolytic cells throughout the gustatory division and cephalic half of the general visceral division of the nucleus tractus solitarii of the opposite side from the lesion; but no more than the normal number of chromatolytic cells are visible in the commissural or caudal half of the general visceral division of this nucleus. The caudal or commissural half of the general visceral division of the nucleus tractus solitarii, which apparently does not send axones to higher levels, represents at least three fourths of the bulk of this general visceral nucleus. It may send fibers to the respiratory nuclei of the spinal cord and to the motor nuclei of the medulla.

Two Nissl series in which the nucleus emboliformis, nucleus globosus, nucleus fastigii, and practically all of the corpus restiforme fibers from one side were destroyed, show no chromatolysis of the cells of any part of either nucleus tractus solitarii or the nucleus commissuralis.

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1. The growth impulse of the cord is normally around three times as great as that of the brain.

2. Although the growth impulse of both brain and cord is less in the females than in the males the relative strength of that of the cord to that of the brain is the same as found to exist in the males. Hence, the relative growth of brain and cord is a specific characteristic independent of sex.

3. When the thyroid apparatus was removed a marked decrease in the strength of the growth impulse of both brain and cord took place. The extent of this diminution was greater in the case of the brain in both sexes, and greater for both organs in the females than in the males. In the male thypars the growth impulse of the cord was nearly six times as strong as that of the brain instead of three times as strong as found in the control rats. In the female thypars the growth impulse of the cord was fifty times that of the brain instead of three times as shown in the controls.

4. The loss of the parathyroid function apparently did not disturb growth ability of brain and cord to a great extent. Further analysis is necessary.

So far there have been no data given which would show the extent of the growth retardation caused by the experimental procedures. This is best obtained through a comparison of the growth of the operated groups with that of the controls, using the growth of the controls as a standard. The details for obtaining the figures for such a comparison are to be found in an earlier paper (4). The results of the computations are given in table 5.

A study of this table reveals the following facts:

In the thypars—

1. The growth of the cord was retarded as well as that of the brain. This holds for both sexes.

2. The retardation of cord growth was much less than was the retardation of brain growth. This also holds true for both sexes.

3. The retardation of the growth of both brain and cord was much greater in the females than in the males.

From this it can be concluded that the brain is more dependent upon the thyroid function for its growth than is the cord.

Donaldson (6) has shown that the percentage of myelin in the spinal cord of a mature albino rat is about twice that of the brain, while the active protoplasmic tissue of the latter is rela-

TABLE 4

The adjusted brain and cord weights for the various groups at 100 days of age, the observed values at 150 days and the absolute per cent increments

	MALES			FEMALES		
	Brain					
	Controls	Thypars	Parathys	Controls	Thypars	Parathys
	g	g	g	g	g	g
At 100 days	1 7140	1 6960	1 6946	1 6515	1 6515	1 6399
At 150 days	1 838	1 7380	1 827	1 7490	1 6550	1 7260
Per cent increase	7 2	2 5	7 8	5 9	0 2	5 3
	Cord					
At 100 days	4175	4049	4039	3963	3963	3877
At 150 days	5170	4650	4910	4760	4390	4560
Per cent increase	23 8	14 8	21 6	20 1	10 8	17 6

TABLE 5

The relative per cent increments from 100 to 150 days of age of the brain weight, cord weight, body length, body weight and tail length of the various groups Controls as base

	MALES					FEMALES				
Group	Brain	Cord	B L	B W	T L	Brain	Cord	B L	B W	T L
Control	100 0	100 0	100 0	100 0	100 0	100 0	100 0	100 0	100 0	100 0
Thypars	34 7	62 2	47 2	31 0	37 2	3 4	53 7	24 5	-28 2	19 4
Parathy	108 3	90 8	64 0	57 1	63 9	89 8	87 6	47 2	20 7	49 3

tively greater than that of the cord. The inherent differences in metabolic procedure as shown by the differences in constitutional make-up, are undoubtedly the foundations for the difference of reaction to the loss of the thyroid.

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CONTENTS

J. B. JOHNSTON. Further contributions to the study of the evolution of the forebrain. One hundred and two figures.... 337

MARION HINES. The development of the telencephalon in Sphenodon punctatum. Thirty-four figures.... 483

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hemisphere and in the formation of its poles, especially the temporal pole; and the earliest recognizable beginnings of the olfactory and the general pallium and the determining factor in their differentiation and development. The point of view from which this work proceeds is that the structural and functional relationships in the adult brain of man or higher animals are to be understood in the light of the evolution of structure in the brain of ancestral forms under the influence of environment and adaptive behavior or habits.

I desire to express my thanks to Dr. Richard Scammon for the loan of his collection of selachian embryos and to Dr. C. E. Johnson for the loan of embryos of Chelydra serpentina.

1. THE CORPUS STRIATUM

The corpus striatum consists of several nuclei and is traversed by important fiber bundles. The globus pallidus is a somewhat conical mass of cells situated deep in the crus, the apex of the cone being turned in the direction of the thalamus. This nucleus is of ancient origin, being recognizable at least in the more primitive reptiles. The putamen is an extensive mass of cells lateral to the globus pallidus, laterally flattened and often much elongated. It is pierced in various ways by bundles of the internal capsule and is bounded externally by the external capsule, outside of which lie the claustrum, the capsula extrema and the insular cortex. The caudate nucleus lies internal to the putamen, occupying the floor of the ventricle and forming a semicircular band of gray matter curving about the internal capsule and extending from the region of the olfactory nuclei in front to the amygdaloid region behind. Closely parallel with the medial border of the caudate is a strand of fibers, the stria terminalis, which relates various olfactory nuclei in front with the amygdaloid nuclei behind.

The following description will show that the stria terminalis in the human embryo and in all lower vertebrates is accompanied by a prominent mass of gray matter which is continuous rostrally with the olfactory nuclei and caudally with component nuclei

of the amygdaloid complex, and that the stria terminalis therefore represents an important primary element of forebrain structure. It and its related gray masses form part of the primitive olfactory apparatus. It is older than the caudate nucleus which overshadows it in the human brain.

a. Nucleus caudatus and stria terminalis

Human embryos. When either serial sections or dissections of the brains of human embryos or foetuses are studied the most striking fact seen in the lateral ventricle is that its floor is formed of two prominent parallel longitudinal ridges. These occupy the place commonly assigned in descriptive anatomy to the corpus striatum, or more specifically to the caudate nucleus. These two ridges appear in the accompanying figures showing sections of the hemispheres in various stages from an embryo of 18 mm. crown-rump length to a foetus of the eighth month. The more medial of these two ridges imbeds the stria terminalis (figs. 1 to 16). The more lateral ridge is closely related to the lateral border of the general pallium in early stages. This is

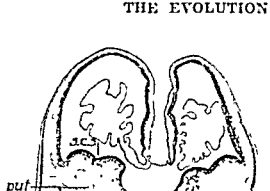
ABBREVIATIONS

a b, basal area in the selachian brain
acc, nucleus accumbens
a l, ansa lenticularis
alv, alveus
am, amygdala
a o l, undifferentiated lateral olfactory area
a p, area parolfactoria
a p a, area perforata anterior
b, basal amygdaloid nucleus
b acc, accessory basal amygdaloid nucleus
b l, lateral part of basal amygdaloid nucleus
b o, bulbus olfactorius
b p, basal proliferation in human and reptilian embryos
c, central amygdaloid nucleus
c a, commissura anterior
c c, corpus callosum
c d, cortex dorsalis
c e, capsula externa
c f, columna fornicis
c g l, corpus geniculatum laterale
c h, commissura hippocampi
c i, capsula interna
ch, chiasma opticum
cl, claustrum
c l, cortex lateralis
c m, corpus mammillare
cort, cortical amygdaloid nucleus
c r, corona radiata
crus, crus cerebri or lateral forebrain bundle
c s, commissura superior
c st, corpus striatum
d b, diagonal band of Broca
di, diencephalon
d v r, dorsal ventricular ridge
f, fornix

directly comparable with the dorsal ventricular ridge of turtles, development of which was described six years ago (Johnston, '16 b). This ridge forms in the adult the greater part of what has been known as the caudate nucleus. This origin of the caudate and its homology with the dorsal ventricular ridge of the turtle and the significance of the bed of the stria terminalis were presented in a paper read before the American Association of Anatomists in 1917, of which the following abstract was published in The Anatomical Record ('18).

> The caudate nucleus consists of two parts, ventral and dorsal, which are distinct in structure and origin and in functional relations. The ventral portion is closely related to the olfactory and parolfactory nuclei, the bed of the anterior commissure and the medial part of the amygdaloid complex. The dorsal portion forms the chief part of the ridge which in man is called the 'tail' of the caudate nucleus. It is closely related to the lentiform nucleus, especially behind the internal capsule where these two enter into a common mass lateral to the amygdaloid complex.
>
> The ventral portion is a part of the olfactory apparatus throughout the vertebrate series. The dorsal portion becomes prominent first in the reptiles where it forms the dorsal ventricular ridge. Its development in reptiles and mammals shows that it is derived from the lateral border of the pallium. The dorsal portion has fiber connections with the internal capsule and the pallium.
>
> The stria terminalis is a complex bundle connecting the rostral and caudal parts of the olfactory apparatus. It and the gray mass in which it is imbedded (ventral portion of caudate) have been greatly elongated in mammals on account of the increased volume of the internal capsule.

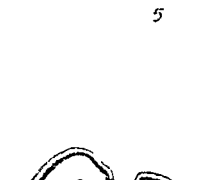
In an illuminating discussion in 1919, Elliot Smith emphasizes the derivation of the body which I have called dorsal ventricular ridge from the cortex in Sphenodon and points out that he had observed this in 1897 and made reference to it in 1902 and in 1910. The statement in the latter place (Arris and Gale Lectures) is very brief and is not accompanied by figures or description so that its significance was not clear to the present writer. Professor Smith states ('19, p. 288): "One fact in connection with this discussion I did not appreciate until a few months ago. The hypopallium of reptiles persists in the mammalian brain where it forms the greater part of the caudate nucleus and of the putamen of the lenticular nucleus, the globus pallidus repre-



5



6



7



8

Figs 5, 6, 7 Transverse sections of the telencephalon of a human embryo of 26 mm C.R. H. 21 Minn Anat × 7 5

Fig. 5 Through the temporal pole. The two ventricular ridges, the internal and external capsules, the pyriform lobe, amygdala and globus pallidus can be recognized.

Fig. 6 Through the bed of the anterior commissure The bed of the stria on the left side contributes to the commissure bed

Fig. 7 In front of the anterior commissure On the right side appear the diagonal band fibers (*p.c.f.*), on the left the ventricle of the tuberculum olfactorium

Figs 8 to 16 Transverse sections of the telencephalon of a human embryo of 33 mm. C.R. H. 16 Minn Anat × 7 5

Fig. 8 Through the caudal border of the internal capsule where the stria terminalis curves around it The stria bed and caudate ridge are separated by a shallow groove, the strio-caudate sulcus

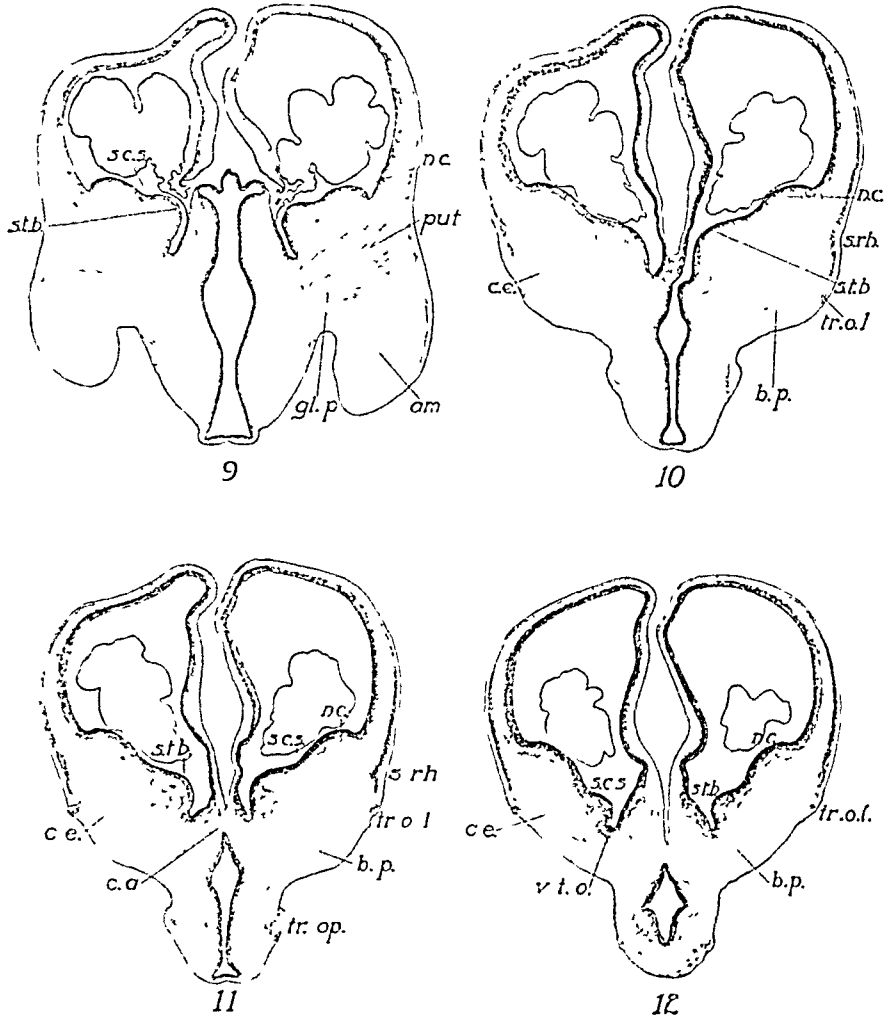


Fig. 9 Through the middle of the crus and the anterior part of the thalamus Note the globus pallidus deeply imbedded in the crus.

Fig. 10 Just behind the anterior commissure. Note the collection of cells in the region of the anterior perforate space and the diagonal band. As in H. 260 these cells are continuous forward with the anlage of the tuberculum olfactorium (fig. 12).

Fig. 11 Through the anterior commissure bed. Note that the bed is continuous at either side with the bed of the stria terminalis. The putamen is identified in the last section and this by its position in the concavity of the external capsule.

Fig. 12 At the caudal border of the tuberculum olfactorium showing its ventricle. The basal proliferation is forming a cortex covering the region of this ventricular pouch just as the tuberculum does in selachians and generally in vertebrates.

senting the major portion of the palaeostriatum In the development of the mammalian brain the phylogenetic history of the corpus striatum is clearly revealed" These homologies will be

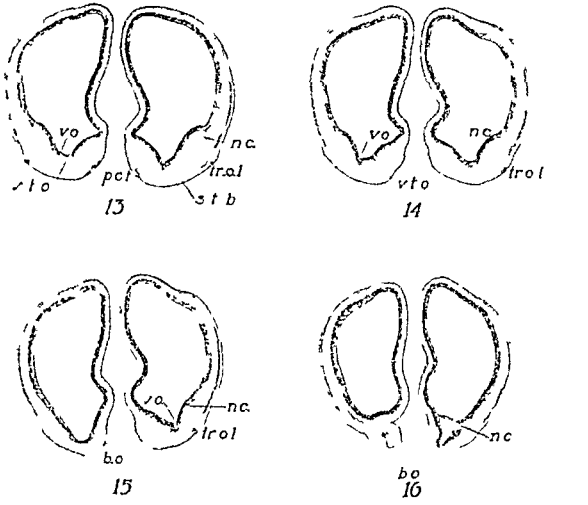


Fig 13 At the rostral border of the precommissural fiber system Note that the striatal bed is shifting toward the medial wall tending to obliterate the ventricle of the tuberculum From here forward the strio-caudate sulcus (labeled *ro* in this figure) leads into the ventricle of the olfactory bulb

Fig 14 Just behind the olfactory peduncle The striatal bed has passed into the medial wall The strio-caudate sulcus descends in the next few sections into the olfactory ventricle

Fig 15 At the base of the olfactory peduncle

Fig 16 Through the olfactory bulb The caudate ridge enters into the dorsal wall of the peduncle

examined further on It appears that the present writer's announcement in 1918 gave the first indication of the homology of the caudate nucleus of mammals with the dorsal ventricular ridge of reptiles

In the rabbit occasional nerve cells are scattered along the course of the stria terminalis and as the bundle approaches the amygdaloid complex, gray matter appears more abundantly between its fibers and this expands into the large medial and central nuclei. Rostrally cells appear in small masses somewhat behind the bed of the anterior commissure with which these masses fuse. Horizontal sections through the anterior commissure show admirably the continuity of the bed of the stria terminalis with that of the commissure and with the nucleus parolfactorius lateralis and the nucleus olfactorius anterior (figs. 63, 64, 65).

The rat possesses a prominent mass of gray lying over and behind the anterior commissure which might almost be called a special nucleus of the stria terminalis (fig. 19). It consists of a dense collection of cells near the point of contact of the stria medullaris and fornix columns, which is continuous with that mass of gray matter which passes down behind the anterior commissure and follows the fornix column toward the hypothalamus. A short distance behind this point, the gray matter accompanying the stria is reduced to a mere vestige as in other forms. Going forward from the anterior commissure the bed of the stria very clearly continues forward and downward over the medial surface of the anterior limb of the commissure to join the medial part of the head of the caudate and the nucleus accumbens.

In the bat (Myotis) for some distance dorso-caudal to its point of contact with the anterior commissure the stria terminalis is imbedded in a large gray mass, much larger relative to the size of the brain than in any other form studied. Then where the stria passes over the internal capsule and is pressed upon by the fimbria it is slender but still accompanied by cells. The stria expands into the medial nucleus of the amygdala as in other forms described.

In the opossum the very large size of the anterior commissure makes the paraterminal body seem relatively small. The stria terminalis has nerve cells interspersed among its fibers throughout its whole course (figs. 54, 57, 58), and in some places these appear both in Weigert and cell preparations as small masses

of gray matter At the rostral end the bed of the stria terminalis fuses with the bed of the anterior commissure, which is completely encircled by the fibers of the stria, and continues forward to the nucleus olfactorius anterior as above described. Caudally the

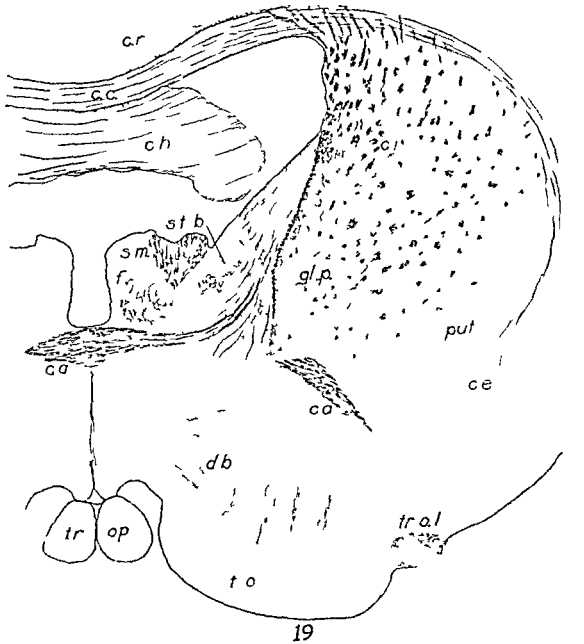


Fig. 19. A transverse section of the brain of the white rat at the caudal border of the anterior commissure. The figure shows the large nucleus in the stria bed above the commissure and the continuity of the stria bed with the bed of the anterior commissure and the gray descending, behind the commissure toward the hypothalamus. Note also the internal capsule bundles scattered throughout the caudate nucleus and putamen.

stria bed expands directly into the medial and central amygdaloid nuclei to which some of the stria bundles are distributed. Other bundles pass into other nuclei, but there is a break of continuity seen in cell preparations, and in Weigert sections these nuclei are separated from the bed of the stria by well defined layers of fibers. Thus in the opossum there is a continuous band or column of gray matter from the nucleus olfactorius anterior to the amygdala, through which run the fibers of the stria terminalis.

In the turtle the stria terminalis is a broad diffuse bundle which lies in a large gray area forming the ventro-lateral wall of the lateral ventricle, beneath the middle ventricular groove. This area was called 'nucleus caudatus' in my paper on the forebrain of the turtle ('15 b) and was labeled *n.c.* in all the figures. Two of the sections shown in figures 15 and 18 of that paper are redrawn and reproduced here as figures 17 and 18. The reader should compare these figures in order to understand clearly the new interpretation which is presented here. It was not until the embryology of the dorsal ventricular ridge was studied ('16 b) that the writer recognized the true homologue of the caudate nucleus. A preliminary statement of the interpretation here presented was published in 1918. The dorsal ventricular ridge of reptiles forms most of the nucleus caudatus of mammals, while the structure now called stria bed forms part of the head of the caudate and the bed of the stria terminalis.

To clearly identify the homologue of the bed of the stria terminalis in fishes it is only necessary to compare a cross-section of a human embryo through the region of the tuberculum olfactorium (figs. 7, 12) with a section in the corresponding region of the embryonic or adult selachian brain (Johnston, '11 a, figs. 17, 18, or Holmgren, '22, fig. 21). In the human embryo there is a sharp depression of the ventricle which forms as above noted a pouch especially related to the olfactory tubercle. The same thing exists in the selachian brain. The tuberculum is much more extensive in the selachian than in the mammal but in both its lateral border comes into contact or continuity with the lateral olfactory area (gray accompanying the lateral olfactory tract, anterior part of lobus pyriformis of Elliot Smith). On the ventric-

ular surface, the structure which lies lateral to the ventricular pouch of the tuberculum in the selachian certainly corresponds topographically to the bed of the stria terminalis in the human embryo. This area in the selachian is a secondary olfactory center and corresponds to the lateral olfactory nucleus and the lateral part of the tuberculum on the external surface. For all practical purposes it is proper to regard this area as the ventricular aspect of the lateral olfactory nucleus. This area extends in the selachian forebrain throughout the length of the lateral olfactory nucleus. No distinct stria terminalis has been described in it but if it contains any association fibers connecting anterior olfactory nuclei with the caudal part of the lateral nucleus, such fibers would constitute a stria terminalis.

From this description it appears that—

1. The stria terminalis is imbedded in a mass of gray which primarily connected the anterior olfactory area with the region in which the amygdaloid complex develops.

2. This gray mass occupies the ventricular part of the ventrolateral wall of the lateral ventricle in the selachian and may be regarded generally as the ventricular or deep portion of the lateral olfactory area.

3. The stria terminalis includes a commissural bundle for the nuclei of the lateral olfactory tracts, and fibers connecting the amygdaloid complex with the parolfactory nuclei and the hypothalamus. (A more complete analysis and description is given below.)

4. The bed of the stria terminalis includes part of what is known in human anatomy as the head of the caudate.

5. The caudate (exclusive of that part related to the stria terminalis) does not appear in fishes but first makes its appearance in the primitive reptiles as a prominent ridge projecting into the dorsal part of the lateral ventricle from the lateral wall. In the turtles this ridge has nothing whatever to do either with the nucleus accumbens or with the mass in the lateral wall with which the nucleus accumbens is related. The latter mass is the bed of the stria terminalis and is separated from the caudate ridge by a deep ventricular groove. In mammals the two bodies come

where the anterior commissure passes beneath it to reach the external capsule in which the temporal branch of the commissure runs back. The portion of the putamen behind this notch is much smaller than the portion in front of it. The anterior portion of the putamen continues on forward and downward in contact with the anterior limb of the internal capsule, the deep lateral gray of the olfactory tubercle and certain scattered but large and important gray masses related to the diagonal band of Broca. These masses push back following the anterior commissure and laterad between the commissure and the anterior part of the putamen into contact with the external capsule beneath the insular pallium. The posterior portion of the putamen remains separated from the amygdaloid complex by the posterior border of the internal capsule. Along the medial surface of the anterior commissure bundle the putamen comes into contact with the most caudally placed masses of cells belonging to the diagonal band (figs. 95, 96). At the extreme temporal angle of the putamen it becomes broken up or subdivided by the bundles of the internal capsule and enters into connection with the enlarged tail of the caudate by thick bands of cells passing between these bundles.

In younger foetal brains the putamen bears essentially the same relations. In the 145 mm. foetus the putamen comes into closer relations with the amygdaloid complex and with the tuberculum olfactorium than in the eight-month foetus. In this younger foetus the putamen extends forward beyond the base of the olfactory peduncle. In all the foetal brains the appearances strongly suggest that the internal capsule bundles do not pass between two essentially distinct and independent nerve centers, the caudate and the putamen, but that these two are rather one continuous body which is pierced by the bundles of the internal capsule. Throughout the whole width of the internal capsule the compact bundles composing it leave spaces between them which are filled by cords or bands of cells which fuse indistinguishably with the caudate above and the putamen below. There is no conspicuous difference in the size, appearance or arrangement of the cells above and immediately below the internal capsule.

This appearance of essential continuity and similarity of the caudate and putamen suggests study of their embryological origin and their relations in lower animals. In human embryos the caudate and putamen can both be clearly recognized at least as early as the stage of 26 mm (fig. 6). At this stage the external capsule is already clearly formed and the representative of the putamen lies just within or medial to it. The next younger embryo available which is well preserved is 18 mm. in length. Four sections from this are shown in figures 1, 2, 3, 4. The external capsule is not developed but the internal capsule and crus are to be seen. Beneath the internal capsule (figs. 1, 2, 3) appears a dense proliferation of cells from the ventro-lateral angle of the ventricular wall which goes to form the tuberculum olfactorium and extends far back toward or into what will be the temporal pole (p. 369). Above the internal capsule and between it and the two ventricular ridges (stria bed and caudate) is another dense cell mass which may represent the globus pallidus. It is surrounded by an extensive area of cells less compactly arranged. Proliferation of cells is going on from both the ventricular ridges, and from the pallium cells seem to be migrating down to the basal or striatal area. The future putamen is doubtless present in this diffuse cell area but this embryo does not show its origin with any certainty. In an embryo of 13 mm. the two ventricular ridges are slightly marked. There is a continuous band of proliferated cells outside both ridges and cells are coming from both ridges and from the border of the pallium.

From the human material at my disposal I am inclined to believe that the lentiform nucleus is laid down by the earliest proliferation of cells in the lateral wall of the hemispheres (before the 13-mm. stage) and that it may receive later additions by cells migrating from the lateral border of the pallium and possibly from the caudate ridge.

If these surmises are true, there is a significant resemblance between the caudate nucleus and the putamen to the extent that the latter is derived from the lateral part of the primary general pallium. There is a distinct difference in that the putamen

seems to be formed chiefly from an earlier proliferation of cells, even before the ridge which gives rise to the caudate nucleus can be recognized.

It is worth while to examine the relations and structure of the putamen in lower mammals and a marsupial. In sections of the rabbit brain stained with neutral red which show the general disposition of medulated tracts and demonstrate admirably the size, form and arrangement of the nerve cells, together with their chromatin content, I can see no clear distinction in structure between the caudate and the putamen. Both consist of small cells diffusely scattered without regular arrangement and of larger, more deeply stained cells which are also unevenly scattered through both nuclei. Many bands of cells connect the two bodies through the internal capsule and the two are continuous at the caudal end near the amygdala. In one respect the putamen of the rabbit differs markedly from that of the human foetus: the anterior commissure passes beneath the anterior border of the putamen to reach the external capsule in which it turns caudad, so that the part of the putamen behind the anterior commissure is much larger than it is in man.

The rat has an unusually diffuse arrangement of the internal capsule bundles (fig. 19). The bundles spread through the whole corpus striatum to reach the corona radiata. The largest and most closely packed bundles rise up through the internal part of the corpus striatum near the ventricle. Here, where one looks for the caudate nucleus as an area of gray matter free from large internal capsule bundles, there is no gray free from fibers, but instead the largest bundles. There is no line of demarcation between caudate and putamen, but the globus pallidus is vaguely indicated by the arrangement of fiber bundles.

In sections of the brain of the bat (Myotis) stained with a cell stain (neutral red) one can speak only of a common or combined caudate-putamen. There is no difference in the appearance or arrangement of the cells throughout the area and there is no separation into two bodies or masses. The internal capsule passes through the common gray mass in many bundles diverging like the rays of a fan. Farther caudally, at the level where the

stria terminalis turns ventrad around the caudal surface of the internal capsule, the caudate-putamen appears as a somewhat comma-shaped mass bounded laterally by the relatively very large lateral nucleus of the amygdaloid complex and the pallium; and medially by the ventricle and the expanding bed of the stria terminalis adjacent to the medial and central amygdaloid nuclei (fig. 77). Forward from the anterior commissure again there is only a large common mass bounded by the external capsule laterally and containing flattened bundles of the internal capsule.

Cell preparations of the brain of the opossum show the caudate nucleus and putamen at the level of the anterior commissure to hold very much the same relations as in the bat (figs. 57, 58). There is no distinction as to size or arrangement of cells and the internal capsule is divided into many bundles between which the gray matter is continuous. The internal capsule has a smooth and regular outline toward the caudate and is denser on that side, while toward the putamen it is broken up into several larger and smaller bundles. It appears as if the internal capsule traverses the putamen rather than the caudate nucleus. Forward from this level the putamen rapidly diminishes so that at the rostral border of the anterior commissure (fig. 59) it is only a small area through which the more lateral bundles of the internal capsule rise to the pallium. Behind the anterior commissure (figs 57, 58) the putamen is larger for a time and is bounded medially by the internal capsule and the globus pallidus. Farther back the putamen grows smaller, becomes wedged in between the central and lateral nuclei of the amygdaloid complex and at the same time fuses with the tail of the caudate nucleus.

In Weigert preparations many small fascicles are seen turning up from the internal capsule to spread out in the caudate nucleus. The same is true of the putamen, although it is not so conspicuous because of the large bundles which pass directly through it. The fiber arrangement gives a distinctive appearance to the lower and caudal part of the putamen adjacent to the globus pallidus.

In turtle embryos as previously described (Johnston, '16 b, '18) at the same time that the dorsal ventricular ridge, the homologue of the caudate, makes its appearance, there is formed quite independently and ventro-lateral to it an active proliferation of

differentiation of the future nucleus caudatus but the assumption is that it is represented in the lowly organized, dorsal general pallium, from which it is derived in the reptiles. This would leave the body in the lateral wall of the telencephalon of selachians to be interpreted as either putamen or putamen plus globus pallidus. The following discussion of the globus pallidus will lead us to include it in this undifferentiated somatic area in the selachian.

c. Globus pallidus

It is not necessary to describe the relations of the globus pallidus in man or typical mammals. The characteristics which are most important for comparative study are the large size of its cells and its close association with the deep part of the internal capsule. While the upper (inner) bundles of the capsule are compact and pass over the globus pallidus, the lower (outer) bundles are infiltrated with cells which constitute the globus center. These cells are conspicuously larger than those of the putamen and in my neutral red preparations usually take a deep stain of a purple hue. Figures 66 and 30 to 35 show the fiber arrangement in the rabbit and the opossum respectively. In the human foetus there is a clear distinction between the outer and inner portions of the globus pallidus. In the outer portion the fibers of the internal capsule are less compact and there are large nerve cells scattered irregularly, together with a large number of glia cells. This portion is pale compared with the putamen with its closely packed nerve cells and occasional fiber bundles. The inner portion is much more pale because of the compactness of the deep part of the internal capsule and because the glia elements are much less numerous. The large nerve cells are at least as numerous as in the outer portion and there are occasional dense clumps or clusters of them.

In the rabbit there is not so clearly marked a distinction between the inner and outer portions, but they can be recognized. The outer portion is marked by longitudinal fibers interlaced with the bundles of the internal capsule. The cells are disposed with their long axes parallel with these longitudinal fibers. Most of the cells of the globus pallidus are of about the same size as the large cells in the putamen above mentioned. In addition there are

present a considerable number of cells of much larger size. These are found in both outer and inner portions but are most numerous along the margin of the globus next the putamen and there is an especially large collection of such cells near the caudo-lateral angle of the globus (fig. 66). At the rostro-ventral border of the internal capsule the cells of the globus are scattered among the fiber bundles and bring the globus pallidus into close relation with the preoptic region. The basal portion of the globus really follows the crus down into the thalamus. Anteriorly there is a large elongated collection of large globus cells medio-caudal to the temporal limb of the anterior commissure (fig. 67) which is directed toward the gray of the diagonal band, but never comes into contact with the latter. Following horizontal sections from above downward, as the diagonal band spreads toward the temporal pole to reach the amygdaloid complex the globus pallidus recedes and remains in close relation with the crus. Its most basal portion is closely applied to the optic radiations and extends medially along the anterior border of the crus into continuity with the gray of the hypothalamus. Finally, the large globus pallidus cells continue in large numbers along the optic radiations to the caudal border of the internal capsule where the putamen and nucleus caudatus fuse. Here the large cells are found among and on both sides of the optic radiations, coming thus into contact with the bed of the stria terminalis and the tail of the caudate. Large globus pallidus cells are found as far ventrally in the sections as internal capsule bundles and nearly as far as the putamen is recognized. They thus come into close relation with the medial and central nuclei of the amygdaloid complex, but should not be confused with them.

In the opossum the globus pallidus holds relations very similar to those in the rabbit. Following a series of transverse sections from behind forward we find beneath the caudal border of the internal capsule (fig. 55) immediately lateral to the stria terminalis bundles and between them and the fused putamen-caudate, a small collection of large cells. These are in immediate contact with the large central nucleus of the amygdaloid complex. Immediately forward this small mass expands into a typical globus

studies of the Dipnoi are available we must regard the caudate as a structure which makes its appearance as a distinct nucleus first in reptiles. It is already so well formed in the most primitive of living reptiles that it seems very probable that it is present in the Dipnoi. In a photograph published by Elliot Smith ('08, fig. 2) there appears a slight thickening of the lateral wall of the hemisphere of Lepidosiren which projects into the ventricle and may be comparable with the dorsal ventricular ridge of the turtle. The caudate in the turtle arises as an infolding of the lateral border of the general pallium. It has the same origin in early human embryos. The caudate is connected with lower centers by both ascending and descending fibers running in the internal capsule. It is therefore to be regarded as an offshoot of or a part of the general pallium, perhaps with functions of a somewhat lower order. This relationship Elliot Smith has expressed by use of the term 'hypopallium.' The caudate and putamen enter into close relations and have a similar structure in mammals, but the two must be regarded as independent nuclei. The grounds for this are that the putamen and globus pallidus are much older phylogenetically than the nucleus caudatus and that the caudate and lentiform nuclei have a separate origin in ontogenetic development.

Functionally the corpus striatum is not a unit. The oldest structures in it, the bed of the stria terminalis and the nucleus lentiformis, are respectively olfactory and somatic sensory or correlating. To the somatic nucleus there is added later in phylogeny a secondary derivative from the general or somatic pallium, the nucleus caudatus which becomes closely related to the nucleus lentiformis both functionally and morphologically. For a clear understanding of the corpus striatum the important points to be emphasized are the derivation of the bed of the stria terminalis from the primitive olfactory centers and its present close relation to those centers, and the late derivation of the nucleus caudatus from the border of the general pallium.

If the terms palaeostriatum and neostriatum are used, it should be understood that the palaeostriatum includes putamen.

globus pallidus and the bed of the stria terminalis, while the neostriatum includes only so much of the nucleus caudatus as is derived from the pallium and excludes that part of the 'head of the caudate' which is related to the stria terminalis, nucleus accumbens and the bed of the anterior commissure.

2. THE TUBERCULUM OLFACTORIUM, DIAGONAL BAND, AND ANTERIOR PERFORATE SPACE

In selachians the medial olfactory area is very much larger than the lateral, extending from the peduncle around the lower half of the rostral wall and in the medial wall back to the anterior commissure. The great reduction of this area in higher forms is correlated with the movement of the olfactory bulb and peduncle from a lateral to the rostral position. There is a large saucer-shaped basal area whose borders meet the medial and lateral olfactory areas medially, rostrally and laterally, while caudally it ends at the level of the anterior commissure. I have named this basal area ('11 a, p. 9) because of evidence that it represents more than the tuberculum olfactorium of mammals.

In reptiles and mammals the medial olfactory area becomes very much reduced while the lateral area becomes relatively more important and gives rise to the pyriform lobe, a great center for correlation with the general pallium. From the medial olfactory area of the selachian brain have been derived the medial parolfactory nucleus and possibly the anterior olfactory nucleus. The anterior olfactory nucleus is a body lying at the base of the olfactory peduncle which varies greatly in size. In the turtle ('15 b) there is at the base of the peduncle a single massive nucleus forming the floor of the ventricle and covered basally by the tuberculum. The depression of the floor of the ventricle into a deep groove in the tuberculum divides this single nucleus into the parolfactory area and the lateral body which forms part of the head of the caudate and which is described in this paper as the bed of the stria terminalis. A deep massive nucleus having the same relations is found in the opossum. In the medial wall in contact with this nucleus and between the tuberculum and the primordium hippocampi is the medial parolfactory nucleus (figs. 60, 61). Probably both of these have

the diagonal band. In mammals this consists of a thin plate of closely packed cells which extends from a point rostral to the anterior commissure down in front of the optic chiasma and caudad on the latero-basal surface to the amygdaloid complex." A more detailed description follows:

In a horizontal section which cuts the hippocampal commissure near its lower border a small collection of very darkly stained cells is seen in close relation to the precommissural fornix (fig. 62). The cells on each side form a continuous column from this point to its fusion with the amygdaloid complex. Lower in the medial wall the paired nuclei are flattened against one another in the median plane. The cells of this nucleus are not small as in the turtle, but distinctly larger and more deeply stained than those of the parolfactory nuclei. They lie intermingled with a mass of fibers part of which come from the medial olfactory tract and nuclei (fasciculus marginalis) and part from the medial forebrain bundle and the diagonal band. The whole system of fibers is the precommissural system of Elliot Smith.

In sections through the anterior commissure (figs. 64, 65) the nucleus thickens at its caudal border while its anterior border remains thin and lies in the course of the fasciculus marginalis. One would think from these sections that this tract passes through the parolfactory nuclei to be related chiefly to this nucleus. Opposite the lower border of the anterior commissure (fig. 66) the two nuclei form a large triangular area and each nucleus comes to the surface in the median sagittal fissure. From this point basalward the column of cells and fibers may be seen on the surface of the entire brain and corresponds to the gyrus subcallosus of the human brain. It should be noticed that between these nuclei and the anterior commissure there is a mass of small cells belonging to the commissure bed and continuous at either side with the bed of the stria terminalis and nucleus accumbens.

In a section close to the base of the frontal pole (fig. 67) passing through the tuberculum olfactorium, the nucleus of the diagonal band is more rounded and is very distinct in structure from either the tuberculum or the paraterminal body. Its cells are mostly large, are closely packed and deeply stained, while those of the

surrounding nuclei are smaller and paler The fissura prima bounding the diagonal band in front is now clearly marked

In a section through the preoptic recess the diagonal band lies fully exposed in the sagittal fissure Its fibers appear to enter into the medial forebrain bundle which here passes backward as a broad band from the tuberculum olfactorium and the parolfactory area The cortex of the tuberculum seems to extend from the fissura prima around to the sulcus endorhinalis where it meets the pyriform cortex. The lateral part of this is primitive olfactory area, not differentiated as tuberculum, and belongs to the anterior perforate space Large cells which lie close to the tuberculum cortex are here seen scattered among the fibers of the medial forebrain tract because this section passes so near the surface of the tuberculum

From this level the diagonal band bends latero caudad and rapidly extends toward the temporal limb of the anterior commissure The diagonal band partly crosses ventrally of the medial forebrain tract, partly is interwoven with it The cells form an elongated area and some isolated clumps are seen near the anterior commissure The only cells with which these could be compared are the large cells of the globus pallidus, but these recede as the diagonal band advances in this region so that there is no doubt as to the limits of either As the olfactory tubercle disappears from the sections the diagonal band grows broader and fills most of the area between the preoptic recess and the sulcus endorhinalis The surface, however, from the fissura prima to the sulcus endorhinalis is still covered by the cortex of the anterior perforate space which is indistinguishable in appearance from that of the tuberculum The diagonal band cells and fibers now fill nearly the whole area medial to the sulcus endorhinalis and the anterior commissure bundles A few sections farther on the cortex of the perforate space suddenly disappears (fig 68) Now the diagonal band fills the whole space from the preoptic region to the sulcus endorhinalis and the fissura prima has disappeared The lateral olfactory area medial to the sulcus endorhinalis is absent from the level of the preoptic recess to the

join the medial forebrain bundle on its way to the hypothalamus. In figure 95 (x) these same fasciculi are seen to the right of the artery and imbedded among diagonal band cells. This is a tract of considerable importance, many additional fascicles of which appear in adjacent sections (figs. 96, 97, x). Most (perhaps all) of the fascicles join into larger bundles which take a position on the rostral side of the anterior commissure just where it joins the external capsule. Here these bundles descend with the anterior commissure into the temporal pole.

These fibers require further study. They may represent a part of the primitive tractus olfacto-hypothalamicus arising in man from the pyriform cortex, following the temporal limb of the anterior commissure and bending down in the medial forebrain bundle to the hypothalamus. Other bundles related to the anterior commissure will be mentioned in the section on the amygdala (system y, p. 449).

In sections following this the bundles just described (x) are imbedded in a dense mass of diagonal band cells medial to the anterior commissure (fig. 96), and this is continuous with another dense collection at the caudal border of the commissure bundle. This last group comes into direct contact with the putamen whose cells appear only as small granules in comparison with the diagonal band cells. Figure 97, which shows the lowest part of the gyrus subcallosus lateral to the preoptic recess, shows also the extreme extent of the diagonal band nucleus on the medial surface of the anterior commissure and in contact with the putamen. A partly isolated group of cells lies medial to this directly over the central nucleus of the amygdala which will appear here in the following sections. Some fifteen sections below the last (fig. 98) the nucleus of the diagonal band has disappeared except for two small groups of cells between the anterior commissure and the central and medial nuclei of the amygdala which continue about ten sections farther. The superficial fiber layer of the diagonal band continues for some sections in the general direction of the anterior commissure and finally disappears. It seems in this brain to be related chiefly or wholly to the central amygdaloid nucleus.

The basal proliferation of cells seen in early human embryos (18, 26 and 33 mm., figs. 1, 2, 3, 10) referred to on page 379 may now be regarded as a common anlage for the tuberculum olfactorium anterior perforate space and perhaps the nucleus of the diagonal band, these structures forming at first a continuous body extending from the base of the olfactory peduncle to the amygdaloid area in the temporal pole.

In brief summary, the diagonal band consists of a nucleus of gray matter probably derived from the basal area of the selachian brain and intimately related to the medial olfactory area, and of a tract of mostly diffuse fibers. Most of these fibers join the precommissural system and connect the amygdaloid complex with the hippocampal formation. With these are mingled fibers which connect the amygdala and tuberculum olfactorium. Other fibers which mingle with the anterior commissure as they are distributed to the temporal cortex pass through the diagonal band. The diagonal band thus represents the caudal border of the whole system of olfactory centers in the hemisphere (the preoptic nucleus being in the telencephalon medium) and maintains the primitive connection between the lateral olfactory area and the hippocampal formation. The preservation of this connection through all the form changes of the hemisphere is due to the growing importance of the lateral olfactory area and especially its new significance in relation to the general pallium which will be discussed in connection with the amygdala.

3. COMPOSITION OF THE STRIA TERMINALIS

An examination of the connections established by the several bundles of fibers which make up the stria terminalis is desirable before undertaking the analysis of the amygdaloid complex. I shall begin with the opossum as a form which is favorable for study and at the same time presents in fairly complete form the elements typical of the stria in mammals.

Just above and behind the anterior commissure, where the stria bed is large and the bundles are not closely packed, the disposition of the individual bundles can be clearly seen in both

Behind the internal capsule the behavior of these bundles is as follows (figs. 21 to 31). The lateral ventricular bundle (3) bends downward and slightly medially and its fibers spread out in the basal nucleus continuing far forward in it. The deeper lateral bundle (4) bends downward and then sharply backward

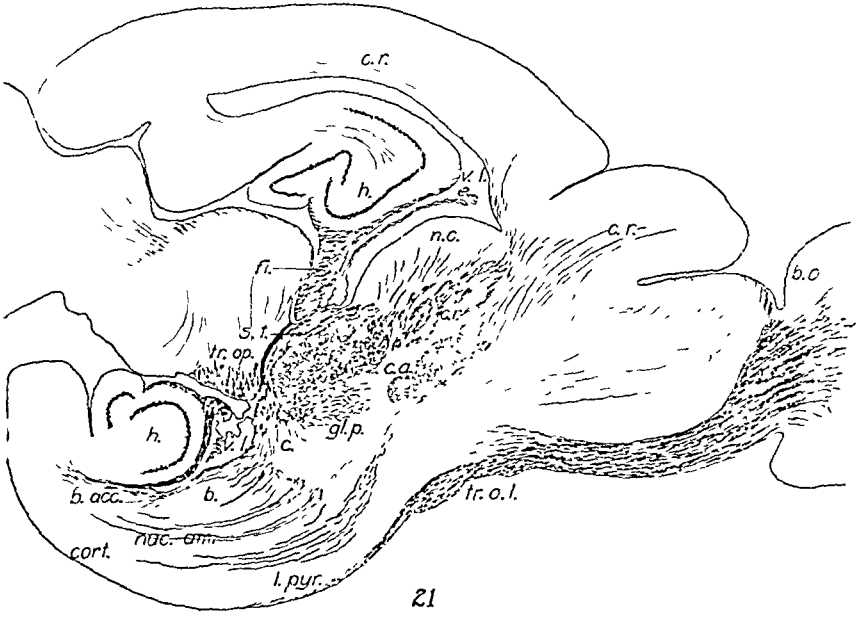
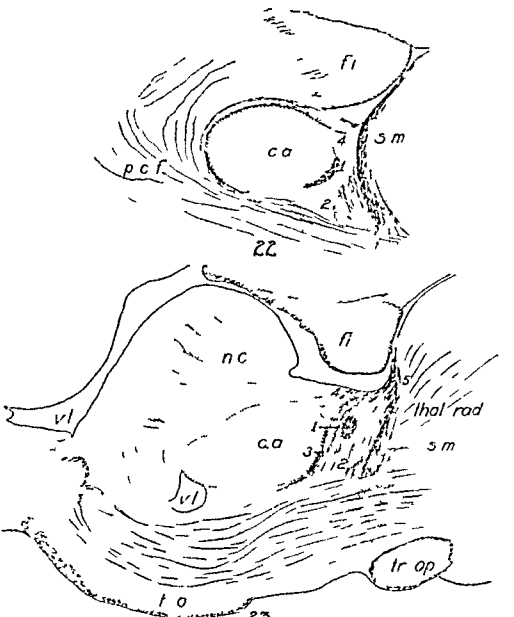


Fig. 21 A parasagittal section of the telencephalon of the opossum to show the general relations of the stria terminalis and corpus striatum. Weigert stain. In this and the following figures the nuclei of the amygdaloid complex are indicated by the last part of the abbreviation without repetition of the letters *nuc.am.* in each case. Where the stria bends around the internal capsule the stria medullaris bundle is drawn in solid black. The distribution of the several bundles to the amygdaloid nuclei is shown in more detail in the following figures. Note the outflow forward beneath the anterior commissure.

between the central and the accessory basal nucleus and is distributed to the accessory basal nucleus back to the point of meeting of this nucleus with the hippocampus. From this nucleus fibers gather and form a bundle running backward and then turning up into the hippocampus at the extreme caudal angle of the temporal pole (figs. 21 and 28). The medial superficial bundle (2) slips down medially on the surface of the brain



Figs 22 to 28 Drawings from another series of sagittal sections of the opossum brain by the Weigert stain The drawings are accurately outlined under the projection apparatus and the stria terminalis system is carefully drawn Other structures are diagrammatically sketched In many drawings the structures labeled *ca*, *ci*, *fi*, *cr* and *tr op* would be nearly black if filled in

Fig 22 A section through the anterior commissure near the median plane Two sections have been combined in order to show bundles 1 and 4 in the same drawing

Fig 23 A section farther lateral when all the bundles are seen in the large part of the stria but dorsocaudal to the anterior commissure The commissural bundle is the dense one imbedded in part of 2 The fascicles of bundle 5 are seen coming out of the stria medullaris Note that a large part of the stria medullaris comes up from the preoptic region from the olfactory nuclei through the medial forebrain bundle

The stria medullaris fibers follow the caudal border of the stria terminalis closely applied to the internal capsule, then descend close to the rostral border of the optic tract so that a close study of both transverse and sagittal sections is necessary to make out their course and destination. As they approach the amygdaloid

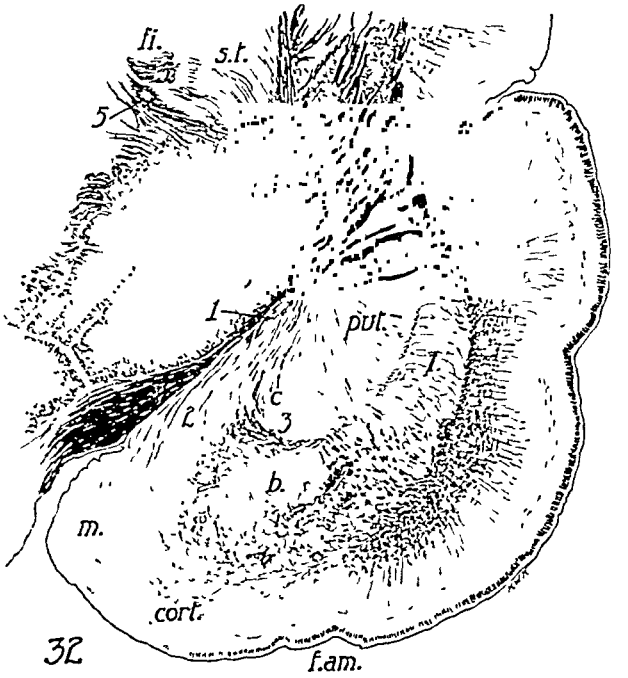


Fig 32 Section 0.9 mm. forward from the last. The stria bed expands into the central and medial nuclei. The stria medullaris bundle (*5*) follows the border of the optic tract. The commissural bundle (*1*) is imbedded in the olfactory projection tract (*2*). Fibers of the longitudinal association system are seen cut across between the lateral and basal nuclei. Compare with figure 55.

complex these fibers form a flattened bundle thicker in the middle and with one thin edge spreading toward the hippocampus and the other directed forward along the lower border of the internal capsule and globus pallidus (fig. 25). Below this point the fibers in both these thin edges separate from the rest of the bundle. The caudal fibers run close along the rostral border of the choroid

fissure, pass beneath the end of the fissure and enter the alveus of the hippocampus. The fibers in the rostral edge of the bundle separate as several small very dense bundles and some of these at least become imbedded in the diffuse fibers of bundle 2 which

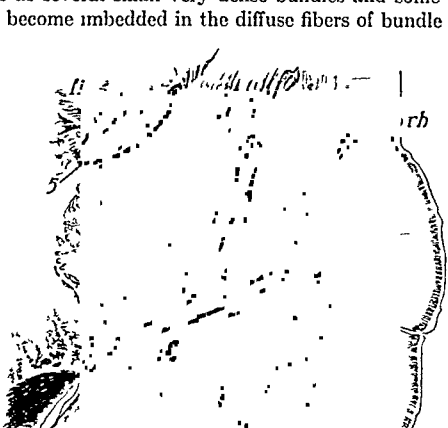


Fig. 33. Section 0.975 mm. forward from the last. In this figure and the next are seen the bundles of fibers coming out of the amygdala and pyriform cortex to connect with the stria terminalis and to go forward beneath the internal capsule and anterior commissure. They are seen especially traversing the basal nucleus and associated with the longitudinal bundle (*l b*). The commissural bundle is now very conspicuous. The stria medullaris bundle (*5*) separates from the optic tract and enters the amygdala. This figure falls between the levels of figures 55 and 56.

turn into the longitudinal amygdalo-pyriform association bundle (fig. 26). They presumably come from the pyriform lobe to go to the habenula. The thicker middle part of the bundle now becomes closely applied to the optic tract and descends to the region of the anterior perforate space. Here they separate from

lateralis and the last by the posterior pallial commissure or tractus corticohabenularis or both (Johnston, '11 a, p. 34, '11 b, p. 521).

The nuclei of the amygdaloid complex mentioned above by names indicating their position will be described in the following section.

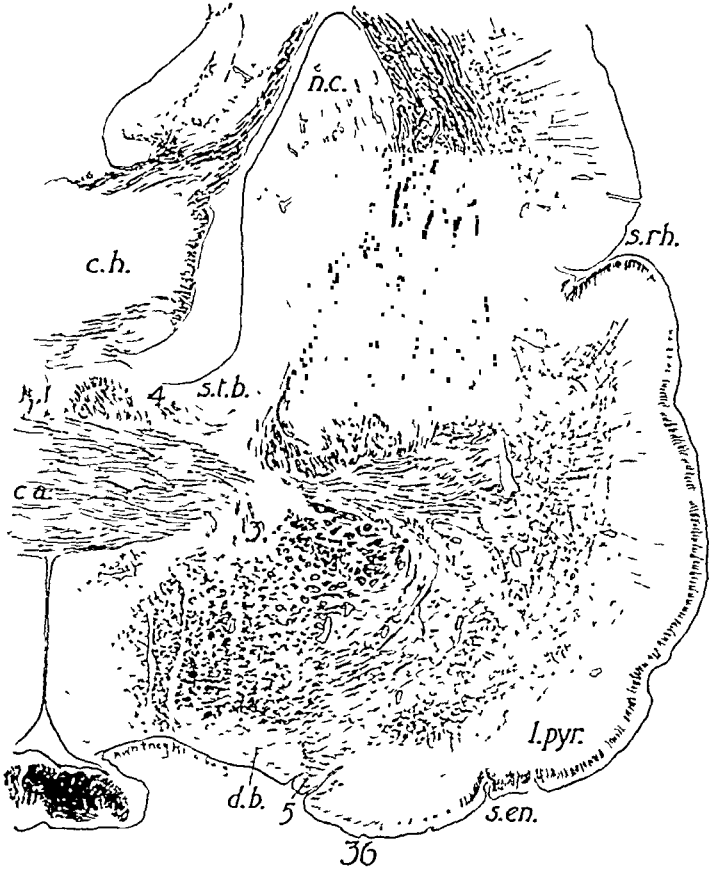


Fig 36 Section through the anterior commissure, 0.75 mm. forward from the last. Bundle *3* of the stria passes forward beneath the commissure, bundle *4* above it. In this and previous figures note the passage of internal capsule bundles through the putamen and the ending of such fibers in the caudate nucleus. Compare with figure 59.

In the rabbit the disposition of the bundles in the region of the anterior commissure closely resembles that in the opossum The commissural bundle is much smaller in the rabbit The supra-commissural bundle is large and shows several separate fascicles. These run farther forward than in the opossum and transverse sections give the impression that more fibers in the rabbit end in the parolfactory region. Caudally the bundles to the medial and central nuclei are the largest, the commissural and stria medullaris bundles and the bundles to the basal nuclei behave as in the opossum. Not many medullated fibers seem to go to the lateral nucleus My rabbit preparations are not suitable for a more detailed analysis of the fibers.

Human foetal brains prepared with ordinary histological stains are of course unsuitable for the study of the fiber tracts in detail. In the region of the anterior commissure only the infra- and supra-commissural and the hypothalamic bundles can be recognized In the amygdaloid complex the distribution of the stria to the several nuclei is clearly of the same type as that seen in the opossum and the rabbit.

In the turtle the following bundles have been described (Johnston, '15 b): First, a commissural bundle related to the small-celled nucleus, which was described as continuous with or as including the nucleus of the lateral olfactory tract; second, a broad bundle surrounding the commissural bundle and connecting the chief (small-celled) amygdaloid nucleus with the parolfactory area. Its fibers pass both above and below the anterior commissure. Third, an olfactory projection tract likewise arising from the small-celled nucleus and running to the hypothalamus Fourth, a non-medullated bundle arising from the large-celled medial nucleus, whose destination was not made out.

In the frog Herrick ('21) recognizes a stria terminalis connecting the amygdala with the medial olfactory area

4 THE AMYGDALOID COMPLEX

a General. The amygdaloid fissure

The history of the bed of the stria terminalis treated in a previous section shows that a primary relation exists between at least part of the amygdaloid complex and the olfactory apparatus

them. This central nucleus gives origin to most of the fibers of the hypothalamic bundle as described in the opossum. This is the olfactory projection tract of Cajal.

The amygdaloid fissure. In order to understand the other amygdaloid nuclei it is necessary to examine carefully their mode of formation. The key to this is found in the amygdaloid fissure described by the writer in the turtle ('15 b). An understanding of this fissure and the part it plays in the evolution of the amygdaloid complex is of the utmost importance and this will justify a detailed examination of its relations. The description first given implied that the whole dorsal ventricular ridge was derived from an infolding in the amygdaloid region. In a later paper ('16 b) it was shown that the dorsal ventricular ridge is formed by an infolding along the lateral border of the general pallium. In a preliminary notice ('18) and in the present paper it has been shown that this ridge becomes the caudate nucleus, which arises in the same way in the mammalian brain. In the adult brain of the turtle ('15 b, figs. 4, 10) the caudal part of the ridge projecting into the ventricle is separated from the rostral part by a prolongation of the middle ventricular groove which bounds the dorsal ventricular ridge ventrally. In the embryonic stages studied there was no indication of a separate mass being formed in this region. Probably the embryos studied were not advanced enough to give a complete history of these ridges. There is abundant other evidence that the caudal part is morphologically and functionally different from the rostral part. The caudal part is related to the amygdaloid complex as at first supposed, the rostral part forms the caudate nucleus.

The evidence of morphological independence is found in the mode of origin of the two ridges (or two parts of what appears to be one ridge in the turtle). The rostral part is formed by rapid proliferation of neuroblasts, growth and bulging inward of the lateral border of the general pallium. This takes place above the sulcus rhinalis which marks the dorsal border of the lateral olfactory area or pyriform lobe. The caudal part is formed by a more pronounced infolding of the ventral wall of the temporal pole along the line of the sulcus endorhinalis. This sulcus, as is

well known, lies wholly within the lateral olfactory area. At the level of the nucleus of the lateral olfactory tract, the in-wandering of cells and the external groove which marks it lie between the nucleus of the lateral olfactory tract and the pyriform lobe. Since there exist here an external groove and a corresponding internal ridge and since there is evident in some animals an actual folding of the wall, it may be said that the temporal portion of the sulcus endorhinalis is transformed into a true fissure. The internal ridge or thickening enters into the amygdaloid complex and I have therefore called this the amygdaloid fissure. This fissure is marked by a large external groove in the turtle (figs. 17, 18) and in all mammals studied by a less conspicuous groove. It is shown in figures 52 to 56, 68 to 77, 83, 84, 85. In human embryos and foetuses the fissure is crowded somewhat more toward the medial surface of the temporal lobe but is clearly evident.

The internal ridge in the reptilian brain corresponding to the amygdaloid fissure has been more or less clearly recognized as a body of special significance by earlier authors. C. L. Herrick ('91, '93) called attention to it under the name of occipito-basal lobe. Adolf Meyer ('92) calls this the nucleus sphaericus and describes it as pushing into the caudal end of the long dorsal ridge which he calls lateral ganglion. Edinger ('96) first used the name epistriatum for this body and later applied the same name to various other structures. Kappers ('08) calls the dorsal ventricular ridge 'epistriatum' and the body in the temporal pole 'secondary epistriatum.' From his description of the fiber tracts it does not appear that the two bodies were clearly distinguished. De Lange ('11) in one series of figures of Varanus calls the rostral part of the ridge 'striatum' and the caudal part 'epistriatum' in which the nucleus sphaericus is imbedded. In a second series of figures he applies the name epistriatum to the whole length of the ridge. He describes a connection of the cells in the dorsal part of the ridge with the cortex, but says that the greater part is filled with cells of striatal type. He considers that the whole structure has a striatal character and is derived from the striatum, having attained a secondary connection with the cortex. In Lacertilia and Ophidia the caudal part (that which is

this mass which represents a specialization in the character of its cells or its fiber tracts is the medial portion which was previously called the medial nucleus. This is a group of cells much larger than those of the nucleus of the lateral olfactory tract, lying in the medial part of the amygdaloid ridge lateral to the temporal horn of the ventricle. From this nucleus a compact bundle of non-medullated fibers runs forward quite isolated from other stria bundles, to join these at the caudal border of the internal capsule. The destination of this bundle has not yet been made out.

It is clear that we have here a special amygdaloid nucleus and the following description will show that its homologue can be identified in mammals. Miss Crosby ('17) compared with this her nucleus ventro-medialis in the alligator. This, however, differs in two marked respects from the nucleus medialis of the turtle. The nucleus ventro-medialis in the alligator is composed of small cells like those of the nucleus of the lateral olfactory tract and Miss Crosby states that it gives rise to part of the stria medullaris and to the olfactory projection tract of Cajal, while the nucleus medialis of the turtle is large-celled and does not give rise to the olfactory projection tract. The position assigned to the nucleus ventro-medialis in Crosby's figure 12 corresponds to that of the medial nucleus in the turtle, but farther forward (figs. 9, 18, 21) this nucleus seems to merge with the nucleus of the diagonal band. It seems probable that the medial nucleus is not developed as a special nucleus in the alligator, or that it lies farther dorsally in the amygdaloid ridge.

Herrick ('21) has compared the medial nucleus of the turtle with the amygdala described by him in the frog. But this appears from his description to correspond rather to the whole small-celled area in the turtle including the nucleus of the lateral olfactory tract and the caudal end of the bed of the stria terminalis (see below, p. 464 to 467).

When the brains of marsupials and mammals are studied we find that the expansion of the hemisphere has first in the marsupial produced a broader temporal pole and allowed the amygdaloid complex to spread and flatten out somewhat (figs. 53, 54) and then in mammals has carried the caudal wall of the hemisphere around

beneath the temporal pole so that for some distance the amygdaloid complex in human foetal brains seems to occupy the roof of the temporal horn of the ventricle In all these forms there are to be found in addition to the structures recognized in the turtle two or three distinct areas or cell-masses which owe their origin to further immigration of cells and differentiation in the region of the amygdaloid fissure

b The amygdala of the opossum

As one follows a series of transverse sections from behind forward the first part of the amygdaloid complex to appear is a plate of cells under the temporal horn of the ventricle and separated from the ventricle by the deep fiber layer (external capsule) which is continuous with the corona radiata (figs 29, 52) In this plate are seen many dense clumps or clusters of cells which remind one of the islands of Calleja in the tuberculum olfactorium The outer surface opposite this cell-plate is marked by a slight groove in which the fiber layer formed by the lateral olfactory tract is slightly thickened This groove is the amygdaloid fissure and is continuous forward with the sulcus endorhinalis The layer of olfactory tract fibers covers the whole surface from a point near the medio-ventral angle (hippocampus) to the sulcus rhinalis on the lateral surface As the new cell plate is continued forward it is particularly important to notice that it is separated from the ventricle by the external capsule and that outside of this nucleus is a fairly dense network of fibers from which rise the radiating fibers of the pyriform cortex The new nucleus seems to be imbedded in or to intrude into the deep layer of radiating fibers of the pyriform cortex This plate of cells is not found as a separate nucleus in mammals I, therefore, propose for it the name accessory basal nucleus

A short distance farther forward two other gray masses appear Medial to the nucleus just described the brain wall is thickened by a rapidly increasing number of cells without regular arrangement These cells form an indistinct amygdaloid nucleus which in the opossum remains covered by a cortical layer similar to the pyriform cortex These two adjacent cortical areas are separated

Passing on forward (figs. 32, 55) the amygdala comes to lie beneath the internal capsule and the temporal ventricle disappears. The medial nucleus continues and is a little larger than in figure 54. The central nucleus has greatly enlarged. Lateral to it lies the globus pallidus-putamen. The caudate has fused with the putamen since the last section studied. There is no very sharp boundary between the central and the lentiform nuclei, but in Weigert sections (fig. 33) the fibers radiating from the internal capsule through the globus pallidus show fairly well the location of the latter. There may easily be and probably are associative and correlating connections between the lentiformis and amygdala here; but there is no intimate fusion of the two and there is no evidence that the putamen enters into the formation of the amygdala. The putamen is distinctly richer in myelinated fiber network than the central amydgaloid nucleus. The basal large-celled nucleus is now conspicuous and an important layer of fibers between it and the central nucleus derived from bundle *3* of the stria terminalis extends on forward to supply the basal nucleus. The lateral nucleus is nearly a rectangular body and the accessory nucleus is reduced to a small mass near the amygdaloid fissure.

At the region of the accessory nucleus where so many fibers come into the amygdala from the pyriform lobe and external capsule there is formed a prominent dense bundle cut across in section (fig. 30). This bundle continues for a long distance forward and backward and seems to be composed of fibers connecting the amygdala and the pyriform lobe. Farther forward we shall find a special slip from bundle *2* of the stria terminalis entering this bundle. This slip, however, would form only a smaller part of the bundle in question and since this bundle dwindles away both in front and behind I conclude that this is an amygdala-pyriform association or correlating bundle. It probably contains fibers arising in various parts of the pyriform lobe and ending in various nuclei of the amygdala and other fibers arising in the amygdala and going to the pyriform lobe. It is the 'sagittales Längsbundel' of early authors, but is independent of the bundle connected with the nucleus of the lateral olfactory tract, to which this name has sometimes been applied.

In sagittal sections (figs. 21, 26, 27) this bundle appears more diffuse than in this transverse series. I attribute this to a variation in individuals. The connection of bundle *2* with this longitudinal bundle is seen in figures 26 and 27. There is some indication also of fibers from this region passing forward in the diffuse network beneath the anterior commissure, a condition first seen in man and the monkey (see below).

In all the sections thus far described the amygdaloid fissure has been marked not only by the external groove but by a sharp break in the cortex of the pyriform lobe. The cortical layers turn inward and from the free edges cells seem to be migrating toward the deep nuclei. The actual migrating of cells presumably ended with foetal development, but the shape and grouping of the cells even in the adult gives a picture of the end stages in the formation of those parts of the amygdaloid complex which owe their origin to this infolding and immigration of cells. The medial and central nuclei are distant from the fissure and show no relation to it. The basal nucleus with its large cells also seems to have no close relation to the fissure in the opossum. The cortical nucleus and the lateral nucleus, however, appear to owe their formation to the immigration of cells from the region of the fissure. The cortical nucleus is composed of small cells like those of the nucleus of the lateral olfactory tract and has been the least displaced by the infolding. It may be regarded as a relatively primitive part of the amygdala whose cells have moved inward and medialward as new nuclei were forming by infolding. The indication that cells migrate into it from the fissure is seen in figures 55 and 56.

In the caudal part of the amygdala where the accessory basal nucleus is most strongly developed, this is the cell mass most closely related to the fissure. However it does not appear that cells were migrating into this nucleus in late stages of development. One of the structural characteristics of this nucleus suggests that it is formed early in embryonic development. The dense clusters of cells scattered through this nucleus may be explained on the supposition that the nucleus was formed by either a mass movement or migration of cells at a stage before the

into the amygdalo-pyriform association bundle in which it runs backward and presumably is distributed to the basal nuclei or pyriform lobe or both through the greater part of their length.

The second outflow of fibers from the pyriform lobe takes place beneath the putamen and consists of many bundles which converge into the temporal limb of the anterior commissure. The relations of the anterior commissure will be reviewed later. It is to be noted here that the anterior commissure bundles running back in the external capsule lie on the outer face of the lateral amygdaloid nucleus and may be in part distributed to it. The network of fibers of the anterior end of the amygdala is so complex that one cannot tell to what extent if any the anterior commissure is related to the amygdaloid nuclei here.

Just as the level of the anterior commissure is reached the amygdala comes to an end. The lateral division of the medial forebrain bundle sweeps across the sections to continue forward in close relation to the pyriform lobe and tuberculum olfactorium. The medial division turns into the parolfactory area, a large part of it ascending as precommissural fibers to the hippocampal formation. On the basal surface of the brain the amygdaloid complex is continued forward by the diagonal band of Broca which follows the general trend of the medial division of the medial forebrain bundle.

The amygdaloid complex in the opossum consists of the following six nuclei: medial, central, basal (large-celled), accessory basal, lateral and cortical. In close relation with these is the nucleus of the lateral olfactory tract. With the exception of the medial nucleus the complex is covered everywhere by the pyriform lobe and the nucleus of the lateral olfactory tract, and these are supplied throughout their whole extent with lateral olfactory tract fibers. From the pyriform lobe myelinated fibers in great numbers pierce at least the lateral, basal and cortical nuclei. The medial and central nuclei represent part of the primitive olfactory centers and it may be assumed that they still receive olfactory impressions. Indeed, fibers of the lateral olfactory tract certainly reach the medial nucleus while the central nucleus lies for a long distance directly upon the amygdalo-pyriform association bundle and the fiber network from the pyriform lobe

penetrates the central nucleus It is also possible that olfactory impulses reach these nuclei by way of the diagonal band It is clear to the writer that all parts of the amygdaloid complex in the opossum are brought under the influence of olfactory impressions, directly or indirectly The large-celled basal nucleus perhaps receives the fewest olfactory impulses from the routes above mentioned But the stria terminalis bundle (3) which supplies it comes from the parolfactory region and in all probability carries olfactory impulses to the amygdala, although it may also contain fibers carrying impulses from the medial nucleus to the parolfactory or hippocampal areas

Other impulses entering the amygdaloid complex may come from the pyriform lobe, from the adjacent nuclei of the corpus striatum, or from lower centers through bundles of the stria terminalis Impulses coming from the pyriform lobe are not simple olfactory impulses Since the pyriform lobe has very large numbers of associating fibers connecting it with the adjacent general cortex along its whole lateral border, the impulses passing from the pyriform lobe to the amygdala have already come under the influence of the general pallium Moreover since the deep fiber layer of the pyriform lobe contains these association fibers from the general pallium it is possible that some of these fibers enter the amygdala directly—an hypothesis which can be tested only by experiment For the greater part of its length the amygdala lies in direct contact dorsally with the tail of the caudate nucleus, the putamen or the globus pallidus and for a long distance the globus pallidus and putamen are deeply wedged in between the central and lateral nuclei It would be very strange if there were not an active interchange of impressions between these primarily somatic nuclei of the striatum and the primarily olfactory nuclei of the amygdala

Of the stria terminalis bundles those numbered 2 and 4 in figure 20 run to the hypothalamus and contain the fibers which carry the effective impulses from the amygdala to lower centers Bundle 2 is clearly the olfactory projection tract of Cajal If these bundles contain fibers which carry ascending impulses, these are probably gustatory impulses which in fishes are brought

small fascicles penetrating both the basal and lateral nuclei and mingling with fascicles coming from the stria terminalis. The bundles of the stria destined for the basal nucleus are seen coming down from the caudal border of the internal capsule along the outer wall of the ventricle to its extreme tip. The tail of the caudate is pierced by many corona radiata bundles which distinguish it from the lateral nucleus.

Farther forward the lateral nucleus is pierced by a larger number of myelinated fibers from both the stria and the external capsule. Although the essential relations are the same this nucleus in the rabbit is richer in myelinated fibers than it is in the opossum.

The basal nucleus grows much thicker than it is in the opossum and this is one reason for the lateral nucleus being pushed farther caudad. Also, when the central nucleus appears it is placed much farther dorsad than in the opossum. The area of interlaced fascicles from the stria and external capsule holds the same position in the two forms, between the central and basal nuclei medially and the caudate-putamen and the lateral nucleus laterally (fig. 39). The thickening of the ventral wall which pushes the central nucleus dorsad is due in part to the appearance of the medial nucleus adjacent to the extreme medio-ventral tip of the ventricle. With this is connected the stria bundle which runs down along the lateral side of the ventricle (fig. 39). Going on forward the temporal horn of the ventricle disappears and the amygdala grows smaller. It consists of the central, medial, and basal nuclei to which the remaining fibers of the stria are distributed. Finally the commissural bundle descends through the most anterior part of the amygdala to reach the nucleus of the lateral olfactory tract in the ventro-medial tip of the temporal lobe. At the same time appear the bundles of the temporal limb of the anterior commissure.

For the description of the amygdaloid nuclei in the rabbit I shall employ a series of horizontal sections stained with neutral red. In this series the cells are sharply stained to show the chromophile substance and the fiber tracts have a dull brick-red stain sufficient to enable one to identify the chief bundles.

In following such a series from above downward we come to the basal surface of the frontal pole of the brain before reaching the temporal pole, and the amygdaloid complex is most naturally approached from the side of the olfactory tubercle, anterior perforate space and diagonal band. For the relations in this region see the preceding description (p. 375). At this level only the posterior border of the internal capsule is present in the sections. The area in front of this and lateral to the optic tract is occupied by the putamen and globus pallidus as already described. In front of these is the anterior commissure connecting with the thin external capsule. These relations are shown in figure 67 already referred to in connection with the globus pallidus.

The broad area of gray matter in the diagonal band is bounded laterally by the cortex of the anterior perforate space, the medial border of the pyriform lobe and the anterior commissure. The anterior perforate space is separated from the pyriform lobe by the sulcus endorhinalis in which lies the main bundle of the lateral olfactory tract. The cells of the pyriform cortex are closely packed and are much more deeply stained than are those of the anterior perforate space. From the narrow interval between the two in nearly every section cells seem to be wandering in toward the border of the external capsule at the anterior commissure. Lateral to the anterior commissure and internal to the external capsule back to its junction with the corona radiata are found flattened clumps of darkly staining cells (fig. 68). In some sections there is a continuous plate of such cells all the way from the anterior commissure to the caudal border of the corpus striatum. This plate lies along the inner surface of the external capsule while the claustrum parallels this on the outside of the same capsule.

In sections near the caudal and lower border of the internal capsule the following relations are found (fig. 68). The special cortex of the anterior perforate space has just disappeared. The gray mass of the diagonal band fills nearly the whole space between the lobus pyriformis and the preoptic region. At this region it may be said that the diagonal band merges with the amygdaloid complex. The putamen is an elongated oval bounded

medial to this appears a smaller rounded mass of smaller cells. Between the two is a zone poor in cells, but the two masses form a large ovoid mass lying in front of the lateral nucleus. In front of these is a broad cortical plate extending medially from the medial border of the pyriform lobe. The area of in-wandering cells continues to be clearly visible at the border of the pyriform lobe (sulcus endorhinalis). This broad plate is homologous with the cortical nucleus in Didelphys, while the two masses internal to it correspond to the basal nucleus of Didelphys. Völsch has described these large and small-celled nuclei which he designates T′ and T respectively. He did not find a large-celled nucleus in Erinaceus or Mus. In size, form, and staining properties the large cells present the closest possible resemblance to those of the pyriform cortex. The cells of the small-celled part are paler and closely resemble those of the cortical nucleus. Whether the equivalent of the accessory basal nucleus of the opossum is included in the small-celled nucleus in the rabbit, I am unable to say. It should be noticed that the large-celled nucleus is farther lateral in position in the rabbit than in the opossum. In the absence of any detailed knowledge of differences in their fibers connections I shall speak of the whole mass as the basal nucleus, which consists of large-celled and small-celled portions.

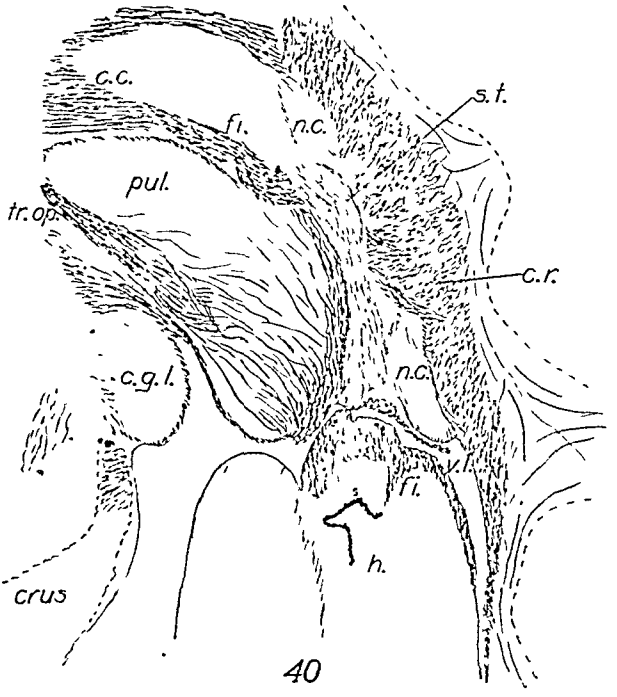
In the following sections approaching the basal surface the lateral nucleus disappears first, then the basal nucleus merges with the cortical layer. Before the basal surface is reached the cortical layer takes on the characters of the pyriform cortex but the sulcus endorhinalis continues to the very end of the series and the appearance of immigration of cells is maintained. The sulcus finally crosses the basal surface of the temporal pole to continue up (dorsad) some distance on the medial surface. Here the appearance of infolding is more marked than anywhere else along the whole sulcus and *the thick bands of in-wandering cells are directly connected with the large-celled basal nucleus* (fig. 73). These facts strongly indicate that the large-celled nucleus was invaginated from the caudal end of the endorhinal sulcus which was carried into the medial wall of the brain by the expansion of the general pallium.

If this is true, it may explain how the large-celled nucleus comes to occupy a lateral position in the mammalian brain while in the turtle the only nucleus of large cells lies next the medial wall. It must be assumed that the thickening of the basal wall to form the cortical and small-celled nuclei took place after the large-celled nucleus had sunk below the surface and these later formations may have pushed the large-celled nucleus lateralward. It is on this basis that the large-celled medial nucleus of the turtle is compared with the basal nucleus in mammals.

Völsch ('06, '11) has distinguished essentially the same nuclei. His nucleus B (and B') appears to be sub-cortical in Erinaceus and Mus and to include the cortex in higher forms. It corresponds to my cortical nucleus. His nucleus D is my medial nucleus, and his D' is the nucleus of the lateral olfactory tract. His nucleus T is small-celled in Erinaceus and Mus but has a large-celled part T' in Foetorius, Lemur and Macacus. His nucleus M is my lateral nucleus, but I cannot accept the merging of nuclei T and M. The two are always sharply separated in the forms which I have studied. Although Völsch has mentioned the appearance of gray in the stria terminalis behind and below the internal capsule and given it the name 'Begleitkern des Stria,' he has failed to appreciate the continuity of this with the medial nucleus or its importance as a bed of the stria terminalis. Völsch also has wholly failed to recognize the central nucleus as one of the chief parts of the amygdaloid complex. He describes a small cell-group E, which he is inclined to think belongs to the amygdaloid complex rather than to the striatum. This cell group undoubtedly is included in my central nucleus, but a large part of the central nucleus is assigned by Völsch to the putamen.

Amygdaloid complex in the bat (Myotis). This small North American bat has an amygdala of relatively enormous size. The bed of the stria terminalis above and behind the anterior commissure is very large like that in the rat. Behind this, where both thalamus and corpus striatum are large the gray is reduced to elongated cells among the stria fibers, but is never absent.

fibers of the stria are deeply stained, the middle layers next the caudate are paler and more diffuse, and the deep fibers next the internal capsule are coarser and more deeply stained. The caudate enlarges slowly forward from this point and more rapidly



Figs. 40 to 43 Sketches from a series of transverse sections of the brain of the monkey, Macacus rhesus, stained by the Weigert method. Figure 40 is the most caudal.

Fig. 40 This section shows the stria as it curves about the caudal surface of the internal capsule and cuts the caudate nucleus twice, above and below the internal capsule. The caudate is very slender at this point in the monkey.

backward, as it descends into the temporal pole. The caudate is traversed by bundles of the internal capsule and small fascicles seem to end in it. Several small islands of gray matter related to the caudate are seen along the corona radiata. Toward the temporal pole the caudate continues to enlarge and these islands imbedded in the corona radiata greatly increase in size. Soon it

is seen that these represent the upper border of the putamen which is imperfectly separated from the caudate by the posterior bundles of the internal capsule.

The stria as it descends toward the temporal pole becomes flattened against the superficial fiber layer of the external geniculate body and its deepest bundle is wedged into the narrow angle between this and the internal capsule. On the face of the external geniculate body is a thin layer of fibers which take a deeper stain than the rest of the stria. This will prove to be the bundle of stria medullaris fibers coming up from the nucleus of the lateral olfactory tract. In sections which pass through the lower border of the external geniculate body the gray bed of the stria begins to increase in volume and the component bundles of the stria are separated.

A few sections farther forward (fig. 41) the bed of the stria expands into a distinct central nucleus, and below it are the medial, basal, and lateral nuclei side by side. The stria passes through the central nucleus and fans out to the three nuclei below. The bundle to the lateral nucleus does not show connection with the stria in this section because just here it bends forward around the ventricle. The central nucleus lies between the optic tract and the putamen. Its upper border is in contact with the lower angle of the globus pallidus.

From this point forward two longitudinal bundles are seen running through the substance of the amygdala. The first lies between the medial and basal nuclei. In addition to fibers for those nuclei it seems to contain the commissural bundle for the nucleus of the lateral olfactory tract.

The second lies between the central nucleus above and the lateral part of the basal and the lateral nucleus below. It corresponds to the sagittal longitudinal bundle in the rabbit. A little farther forward a broad bundle comes down from the stem of the stria through the central nucleus to join this bundle. Many of these fibers run directly down past the longitudinal bundle to spread out between the basal and lateral nuclei (figs. 41, 42, 43). All the while the tangential fiber layer of the pyriform lobe and its connection with the corona radiata hold essentially the same

Opposite the amygdala the external capsule is greatly thickened and is indistinguishably bound up with the corona radiata of the temporal lobe. Toward the anterior end of the amygdala the larger part of the fibers of the corona radiata collect into the anterior commissure and the external capsule, now a thin band, is separated from the corona radiata by the claustrum. As the anterior commissure collects, many bundles and small fascicles run through the lateral amygdaloid nucleus.

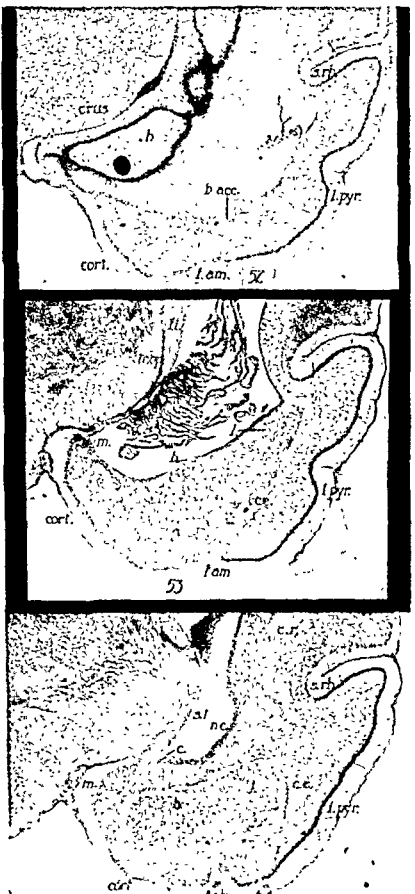
Meantime important changes are taking place in connection with the amygdalo-pyriform association bundle (sagittales Längsbundel). Mention was made of fibers from the stria passing down beneath this bundle to be distributed to the basal and lateral nuclei. Fibers continue in this position so far forward that they can scarcely all be ascribed to the stria. They seem rather to enter a system of fibers directed forward and mesad beneath the globus pallidus. At the same time another rather diffuse bundle rises from the amygdalo-pyriform association bundle, runs in the dividing zone between the central nucleus and the putamen, and joins the same fiber system. These two bundles are shown in figure 43 where they appear like the two elements of a sign of parenthesis (). These fibers run on mesad beneath the globus pallidus and join the general system of precommissural fibers passing up through the parolfactory area. They may be regarded as one of the deep components of the diagonal band fiber system.

Figs. 52 to 61 Transverse sections of the brain of the opossum, Didelphys virginiana from the temporal pole to the olfactory peduncle to show the structure and relations of the corpus striatum, amygdaloid complex, etc. Neutral red. × 10. Sections are 45 μ thick.

Fig. 52 In the caudal part of the temporal pole, showing the accessory basal nucleus as a collection of irregular clumps of cells. The area medial to the amygdaloid fissure (*cort.*) is continuous with the pyriform cortex, but because of its history in mammals it is assigned to the amygdaloid complex.

Fig. 53 Section 1 mm. forward from the last. The medial, basal and lateral nuclei have appeared. Compare with figures 29 to 31 for the position of the lateral and basal nuclei with reference to the external capsule.

Fig. 54 Section 0.6 mm. forward from the last. The lateral and basal nuclei are larger. The central nucleus has appeared and the stria bed descends over the internal capsule to expand into the central and medial nuclei. The immigration of cells at the amygdaloid fissure is evident. The large-celled (dorsal) and small-celled (ventral) portions of the basal nucleus can be distinguished.


crus
.h
b acc.
l.pyr.
cort.
l.am.
m.
l.pyr
cort.
l.am
c.r.
s.rh.
s.l
n.c.
c.
l.m.
c.c.
l.pyr.
cort.
l.ah.

nucleus and the putamen is a network of fibers part of which is condensed into a definite 'sagittal longitudinal bundle.' Parts of this network extend dorsad around either side of the rounded mass in the central nucleus, producing an appearance somewhat like the sign of parenthesis, just as in Macacus. Now from these amygdaloid fibers there is formed in the dorsal part of the central nucleus a distinct bundle which continues forward beneath the anterior commissure, turns mesad and is traced eventually to the tuberculum olfactorium (figs. 85 to 88, *z*). This specific bundle is small and probably contains only a minor part of the fibers which enter or leave the amygdala by this route. It lies in the midst of a rather broad area of diffuse fibers which enters the deep part of the diagonal band system. The more superficial part of this system, in the lower forms studied, is related to at least the central and medial nuclei of the amygdala. Attention is drawn here to the fact that fibers lying deep in the brain, close to the anterior commissure, and connected with the sagittal longitudinal bundle of the amygdala belong to the diagonal band system. This constitutes one of the chief pathways of connection for the lately formed basal and especially lateral nuclei. The fiber tracts connected with the lateral nucleus enter that nucleus by its anterior end. This is what we should expect since we have found it formed in the rabbit and bat by immigration of cells in this anterior region. Evidence of a similar mode of formation in man will be mentioned below.

Forward from the level of figure 85 the basal and medial nuclei rapidly disappear from the sections. The place of the medial nucleus is taken by a rounded medial prominence which probably indicates the position of the nucleus of the lateral olfactory tract (fig. 86). Neither of the fiber bundles related to that nucleus are seen in this brain. The lateral nucleus becomes thin and is more and more broken up by bundles of the anterior commissure passing across it. The central nucleus continues as a large area which merges with the diagonal band.

In this foetus appear certain bundles closely associated with the anterior commissure which descend into the temporal pole mingled with the distributing bundles of the commissure. They

are shown in figures 86 and 87. They cross the preoptic region as if to run up in the precommissural fiber system. They may be a part of the diagonal band fibers which go beyond the amygdaloid complex to be distributed to the pyriform lobe. Or, they may turn into the lateral amygdaloid nucleus. These bundles will be referred to as the system *y*.

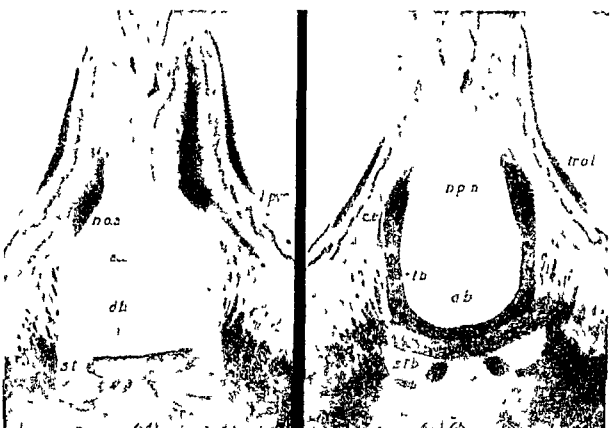


Fig 64 Through the dorsal border of the anterior commissure Only the commissural bundle of the stria terminalis is clearly visible Note that in this figure and the next the stria bed extends forward medial to the anterior limb of the anterior commissure The true caudate nucleus is largely filled with internal capsule bundles as in the rat

Fig 65 Through the anterior commissure Note that the stria bed continues down behind the commissure lateral to the fornix columns This is the bed of the hypothalamic bundle or olfactory projection tract

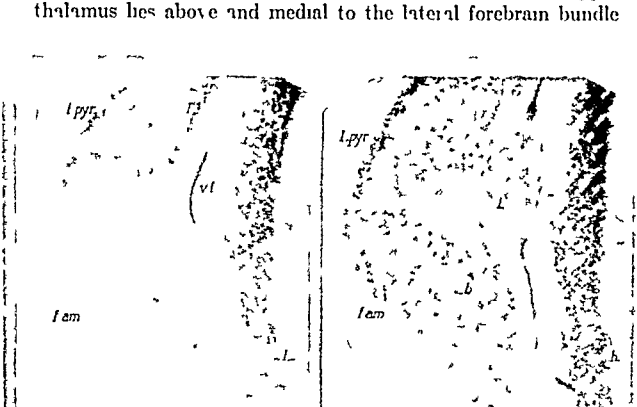
The amygdaloid nuclei of this foetus correspond closely to those of the opossum, rabbit, bat and monkey, namely, a central, medial, a basal which is subdivided, a cortical and a lateral, and these have so far as can be observed in material stained as this is, the same relations to the chief fiber tracts The differenti-

d. Summary of the amygdala

The somewhat detailed review of the nuclei entering into the amygdaloid complex in a marsupial, mammals and man seems to show that there is essential uniformity in these structures. The same nuclei are present and in the same form and relative position. There is one nucleus, the accessory basal, in the opossum not separately recognized in mammals, while the small-celled and large-celled parts of the basal nucleus in mammals are distinctly separated by a lamina of fibers. The position of the nuclei is shifted in two respects. First, between marsupials and the lower mammals the nuclei which occupy the floor of the temporal horn in the opossum are shifted into the rostral wall of the ventricle by the elongation of the hemisphere and the turning downward and forward of the caudal wall of the temporal pole. Second, the nuclei which lie in the following transverse order in the lower mammals, medial-basal-lateral, are shifted in man into a nearly vertical series in which the medial nucleus is most dorsal (high up in the sulcus hemisphaericus) and the lateral nucleus is most basal.

The nuclei fall into two distinct groups from the standpoint of origin and age: the primitive or little modified central, medial, cortical and nucleus of the lateral olfactory tract; and the new nuclei formed by infolding or immigration of cells: basal and lateral. The nucleus of the lateral olfactory tract is a remnant of the primitive lateral olfactory area of fishes which has been maintained as the place of ending of a part of the lateral olfactory tract and which in all vertebrates is connected with its fellow by a bundle of fibers through the anterior commissure. This nucleus is much reduced in primates, but is not wholly absent as Völsch believes. The medial nucleus is also a remnant of the olfactory area of lower vertebrates. It is not differentiated in the reptiles but in marsupials and mammals it appears as a special cell mass derived from the medial and superficial part of the lateral olfactory area. The central nucleus represents the deeper part of the olfactory area. The central and medial nuclei remain always in the closest relation and together give rise to the largest part of the

great olfactory projection tract, connecting the amygdala with the hypothalamus This tract is primitive and is large in fishes, namely that portion of the tractus olfacto hypothalamicus which arises from the lateral olfactory area Its course to the hypothalamus lies above and medial to the lateral forebrain bundle



Figs 75 to 79 Five transverse sections of the brain of the bat Myotis between the temporal pole and the precommissural region to show the relations of the nucleus of the diagonal band and the amygdaloid complex. The photographs are flat because the sections are very thin Neutral red

Fig. 75 Through the caudal part of the temporal pole. × 110 The fissura amygdala is marked not by an external groove but by a broad arching inward and thickening of the cell layers Note the contrast with the pyriform cortex The ventricle is a narrow cleft in the bat This photograph and the next are rotated clockwise in placing on the plate A line passing through *f.am* and *vl* and one through *f.am* and *l* in figure 76 would be parallel with the median vertical plane of the brain

Fig 76 Section 0 1 mm rostral to the last × 110 Continuation of the broad infolding of cells forming a fairly distinct basal nucleus The lateral nucleus appears as a small triangle pushing into the ventricle from the lateral side and nearly obliterating it

and push this fiber layer up on their deep or internal surface, so that it comes to lie between them and the central nucleus. In this region is found an extensive and complex network of fibers, of which the 'sagittales Längsbundel' is part, all of which may be regarded as in a sense a modification of the external capsule. The basal and cortical nuclei remain as a thickening of the basal wall outside of the external capsule. Farther forward, where the anterior commissure enters the external capsule, the cells wandering in from the line of the sulcus endorhinalis took up a position on the internal face of the external capsule between it and the putamen. Here the cells moved upward and backward until the greater part of them occupied a ventricular position behind the putamen as the thick lateral nucleus (opossum, rabbit, bat). This is essentially the position of the lateral nucleus in earlier human foetuses, but in later stages it is carried into a more basal position, as already described. Because of its mode of formation the lateral nucleus comes to be covered over its whole lateral face by the external capsule and it is more closely related to the putamen than the other nuclei are.

When we look for an explanation of this morphological history of the amygdaloid complex in the habits and environment of animals and the functions to be performed, we will find it helpful to reduce the story of its evolution to still more general and broader lines. The formation of the hemisphere, which remains to be discussed later, resulted in bringing an important part of the lateral olfactory area into the temporal pole. This temporal olfactory area was connected with the anterior olfactory nuclei. 1) along the lateral surface of the hemisphere by the elongated lateral olfactory area in which ran the lateral olfactory tract; 2) by a basal area containing the equivalent of the diagonal band, anterior perforate space and the tuberculum olfactorium, and, 3) along the ventricular surface by the deep counterpart of the lateral olfactory area in which ran the commissural bundle and other fibers which we now assign to the stria terminalis. As the expansion of the general pallium pushed the temporal olfactory area farther apart from the anterior olfactory areas, the thickening of the internal capsule caused an arching up and reduction

in volume of the middle part of the gray bed of the stria terminalis There was then a fairly massive temporal area receiving the endings of the lateral olfactory tract and connected with the anterior olfactory areas and other brain centers by fibers running in the stria terminalis, the diagonal band and the stria medullaris This is the general situation which we designate by the term, the amygdaloid area



Fig 89 Through the base of the olfactory peduncle showing the distribution of the anterior limb of the anterior commissure Note the very thick ventricular layers overlying the stria and the caudate The stria bed descends between the anterior commissure and the precommissural fiber system toward the tuberculum The strio-caudate sulcus is homologous with the middle ventricular sulcus of the turtle (cf figs 17, 18)

Fig 90 Section 0 8 mm forward from figure 89 This section shows clearly the independence of the stria bed from the caudate nucleus Here the stria bed extends from the letters *a b* to *s c s* Below *a b* it fuses with the anterior olfactory nucleus which lies upon the tuberculum Note the large island of the tuberculum extending up in the medial wall and compare with a corresponding section in the opossum figure 60

haps the largest of all the sensory areas of the pallium is devoted to this function.

Finally, the significance of the sense of smell has been changed. With the development of the other sense organs the sense of smell became less important in the search for food and became more important as a means of protection against deleterious conditions which might be indicated by odors. Finally, in man olfactory impressions have come to have considerable aesthetic value, giving pleasure or displeasure aside from any material service in maintaining life.

All this and more we imply in speaking of the expansion of the general pallium in terrestrial vertebrates. The forebrain of fishes had a large apparatus for olfactory impressions and for the correlation of these with taste impressions. It had also a considerable area for the reception of at least tactual and visual impressions and means for the correlation of these with olfactory impressions (fiber connections between somatic and lateral olfactory areas). Since there is a large lemniscus system in fishes bringing proprioceptive impulses up to the thalamus, it is probable that these are represented in the thalamic radiations to the somatic area in the forebrain. The needs of land animals brought about the expansion of the tactual, proprioceptive, visual and motor elements and the addition of an auditory element to the somatic pallium. The visual and auditory elements were located in the caudal part and with the final development of border zones and association areas these were pushed into the occipital and temporal poles, respectively.

Now, throughout all these changes in habits and activities on one hand and in brain structure and functions on the other we are interested here in the relations of the olfactory mechanisms to the greatly enlarged somatic pallium having to do with the external relations of the organism to its environment. We have seen that the olfactory centers in the medial wall of the hemisphere have greatly diminished from selachians to land animals, while the lateral olfactory area has developed in relative size and complexity, giving rise to the pyriform lobe as an organ for correlation with the somatic pallium. The morphological evo-

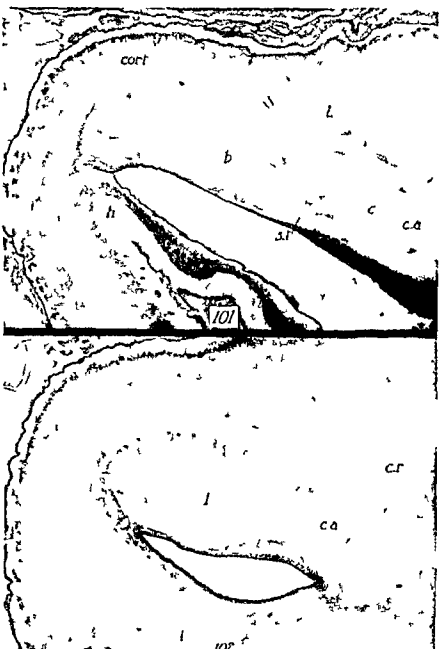


Fig 101 Section 1 5 mm below the last The section cuts through the length of the basal nucleus A remnant of the central nucleus is seen near the anterior commissure Strands of stria and other fibers traverse the basal nucleus to reach the cortical nucleus and pyriform cortex (compare figures 26, 11, 12) The lateral nucleus is represented by clumps of cells which are in reality the tips of the lobules cut off (compare figs 81, 84 85, 102)

Fig 102 Section 2 3 mm below the last The section is near the end of the temporal horn of the ventricle The nucleus (*l*) which is distinctly lateral in position in marsupials and mammals is the most basal in man Note how the anterior commissure bundles cut into and lobulate the lateral nucleus as they enter the corona radiata and spread to the temporal cortex

33. The pyriform cortex adjacent to the general pallium became most directly involved in olfacto-somatic correlation. When vertebrates came to live on land the tremendously increased number, range and variety of stimuli led not only to the great expansion of the general pallium but also to an increase in the centers for correlation of olfactory with somatic impressions. This was the occasion for the formation of the new nuclei out of the pyriform lobe in the manner above described.

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the 19.1 mm. human embryo, number H 173 of the Chicago collection (Hines, '22), can be seen. Beginning at the recess in front of the optic chiasma (*rec. prcop.*), the following structures may be identified: the ventral massive portion of the lamina terminalis, pars crassa (*p. c.*); the dorsal slender division of the same, the pars tenuis (*p. t.*); the angulus terminalis (*ang. term.*), a small portion of the roof, from which no lateral plexus invaginates, the tela chorioidea telencephali medii (*tel. ch. tel. med.*); the paraphysis (*par. ar.*); and the velum transversum (*vel. trans.*). Extending rostrally above the anterior and posterior limits of the paraphyseal arch (*par. ar.*) is the paraphyseal pouch (*p. p.*), while ventral and lateral to this midline structure, the lateral choroid plexus (*pl. ch. v. lat.*) is visible. The roof of the third ventricle extends forward over the paraphyseal pouch and, although not markedly plexus-like in morphology, is ependymal in structure. At its most caudal limit the pineal evagination is attached. In the floor, beginning at the recessus preopticus the following typical hypothalamic structures are found, the optic chiasma, the tuber cinereum, recessus infundibuli, and the recessus mamillaris.

In figure 34, two ventricular ridges in the lateral wall of the hemisphere may be seen, the small, inconspicuous neostriatum, separated from the ventral, larger paleostriatum by the sulcus interstriaticus.

Embryos, Stage PQ, Nos. 50a and 51a (figs. 3, 4, 5 and 6)

The four figures taken for illustration of the development of the telencephalon in Dendy's Stage PQ show at a glance that the cellular differentiation of the various sectors has progressed further than that seen in the preceding forebrains. The dorsomedial area or the primitive hippocampus (*prim. hip.*) lies now almost completely upon the medial wall with its outer layer distinctly cell free. The ventro-medial sector is unusually thickened, laterally, and contains the nucleus medialis septi (*nuc. med. sept.*, figs. 3 to 5). Taking the sulcus superstriaticus (*sul. superstr.*, figs. 3 to 6) for the ventral limit of the dorsolateral sector and the beginning of the cellular outer layer as its

medial boundary, it is clear that this portion of the forebrain evagination is minute. This is the region which contains the dorsal portion of the pyriform, if Elliot Smith ('19) is correct, and whatever of general pallium Sphenodon possesses.

Lying between the angulus ventralis (*ang. vent.*, figs. 3 to 5) and the sulcus superstriaticus is the enormous ventro-lateral area, the region of the striatum. That division of the striatum which lies between the sulcus interstriaticus and the sulcus superstriaticus, the neostriatum, is thicker and more massive than its development as seen in Stage P, number 39a. This enlargement of the dorsal ventricular ridge, the neostriatum, is very evident in the wax model of embryo number 50a, and extends rostrally as far as the enlargement of the vesicle itself.

The division of the telencephalic wall into three cellular layers is most evident in the neostriatum. Here the writer wishes to point out that of these three, the middle layer is the thickest. The outer cortical layer is quite distinct from either the outer mantle layer or inner matrix. Further, the middle layer (*mid. l.*, figs. 3 and 4) of the developing neostriatum is continuous around the sulcus superstriaticus with the middle or intermediate cell layer of the small dorso-lateral sector. In a like manner, the continuity of the mantle layer or marginal zone of the pallium with that of the neostriatum (*man. l.*, figs. 3 and 4) and the matrix of the pallium with that of the neostriatum may be followed around the superstriatal sulcus (*mat.* figs. 3 and 4). The ventral limit of what appears to be an outer cortical layer (*man. l.*) is the space in the neostriatal wall into which the thalamic striatal fiber systems will extend. This peculiar arrangement is not only characteristic of this portion of the forebrain wall in this embryo, but also in the development of the homologous region of the human (figs. 29 to 32, *cor. str. lat.*, Hines, '22).

In figure 6, a section through the foramen interventriculare, the typical arrangement of the invagination of ependymal tissue joining the lateral limb of the paraphyseal arch (*p. a.*) forms the plexus chorioideus ventriculi lateralis. Dorsal to the paraphyseal arch lies the cross section of the forward extension of the paraphyseal pouch, while above the latter is the balloon-like ependy-

chorioidea telencephali medii. Within the tissue itself two nuclei mentioned above are found, the medial and lateral nuclei of the septum. This condition may be seen in the stage of development reached by a 60 mm. human embryo. However, when the same region is examined at the level of the commissura pallii posterior, two triangular nuclei appear lateral and ventral to the commissura, the nuclei of the commissura aberrans (*nuc. c. ab.*, fig. 11).

In the wax model of the forebrain of this embryo, the preoptic recess has increased in depth; the pars crassa of the lamina terminalis has encroached upon the pars tenuis; the paraphyseal pouch has elongated dorsally, while the tela chorioidea telencephali medii remains unchanged. This development resembles that outlined for these same structures in man (Hines, '22).

The approximation of the middle and mantle layers in the brain wall about the sulcus superstriaticus may be easily demonstrated in figure 8 taken from a sagittal series. The other features are similar to the descriptions for number 141. In figure 12 from embryo number 144, two new circular nuclei besides the nuclei medialis et lateralis septi lie in the septum. The more ventro-medial of the two lies dorsal to the commissura hippocampi and may be seen in the same position in a 60 mm. human embryo; the dorsal-lateral one, lying between the medial and lateral nucleus, may also be seen in the same human embryo. In figure 13, the nucleus ventro-medialis extends dorsomedially to the sulcus interstriaticus, which as a group of cells may be seen about that sulcus, in the more rostral levels of this stage of development of the telencephalon. This nucleus may be said to have two limbs, a dorso-medial, which lies along the interstriatal sulcus and a ventro-medial, found in the extreme ventral angle of the forebrain vesicle. These two limbs become confluent in the caudal levels of the telencephalon.

Embryo, Stage RS, No. Sii (fig. 14)

The development of the telencephalon of embryo number Sii resembles in all points that of the adult, except that the neostriatal ridge is not as large as it is in the adult. When the dorsal wall of

the forebrain vesicle is lifted off two huge ridges appear; the lateral neostriatum, which extends from the anterior portion of the olfactory stalk to the most ventrolateral expansion of the telencephalon, and the medial septum. The latter is confined to the medial wall only and does not swing lateral in the vesicle with the hippocampal formation whose most posterior end almost meets that of the pyriform, encircling the ventro-lateral-posterior tip of the neostriatum. If the neostriatal hillock is pushed aside, a small ridge, the paleostriatum, may be seen, making its way, from about the posterior third of the neostriatal formation, anteriorly into the basal portion of the olfactory stalk.

The one figure of this brain (fig. 14) is cut sagittally through the vesicle in such a manner that the greater part of the ridge shown is neostriatal. The anterior portion of the neostriatum contains the definite stratified arrangement of cells; in the posterior part the same cells are more diffuse. Ventral and posterior to the sulcus interstriaticus is a nucleus, which by its position seems to be the lateral anterior limb of the ventromedial nucleus of Crosby ('17). Immediately ventral to the hippocampal cortex, lying among the fibers of the fornix are a few cells, the remnant of the primordium hippocampi. Arching from the pyriform lobe, anteriorly, to the hippocampus, posteriorly, is the irregular cortical layer, the mantle layer of the general pallium.

SUMMARY OF THE DEVELOPMENT OF THE TELENCEPHALON OF SPHENODON PUNCTATUM

The telencephalic evagination of the earliest stage presented resembles that of a 11.8 mm. human embryo. The two halves of the forebrain are joined in the midline, anteriorly by a comparatively slender piece of septum ependymale, posteriorly by a very thin ependymal area in the form of an arch known as the paraphyseal arch. In the dorso-medial portion of the wall of the incipient hemisphere the primitive hippocampus is distinguished from the rest of the vesicle by a relatively clear cell-free outer layer.

The primitive hippocampus characterized by this same peculiarity of cell arrangement is found in the dorso-medial sector.

The septum (*sept.*, figs. 15 to 20) contains two nuclei, the nucleus medialis septi (*nuc. med. sept.*) and the nucleus lateralis septi (*nuc. lat. sept.*) poorly defined, when compared to their diagrammatic outlines in the developing Sphenodon, and traces of the nucleus accumbens of Kappers (*nuc. ac.*, figs. 17 and 18) and the nucleus of the commissura hippocampi (*nuc. hip. com.*, figs. 19 and 20). The cortex of the tuberculum olfactorium (*tub. olf.*, figs. 16 to 18) is present as an ill-defined layer of cells, not at all like the beautifully marked nucleus to be found in Stage R, number 141 (fig. 11).

The striatal complex. The paleostriatum (*paleostr.*, figs. 16 to 21) is the slight ventral elevation which lies between the angulus ventralis (*ang. vent.*, figs. 16 to 21) and the sulcus interstriaticus (*sul. interstr.*, figs. 16 to 21). In the region of the olfactory stalk the ridge fuses with that of the septum and both come to form the ventral sector of the evagination. Caudally the ridge becomes relatively unimportant, so that approximately within two-thirds of the total distance from the base of the olfactory bulb to the tip of the posterior pole of the hemisphere this ridge has disappeared.

It is composed of scattered cells without definite nuclear groupings. In its rostral extent a few cells curve about the angulus ventralis next the diminutive layer of matrix, the nucleus accumbens of Kappers. As a nucleus it is not as prominent as it is in Stage R. In its more caudal position another nucleus curves about its dorsal limiting groove, the sulcus interstriaticus. This nucleus appears to be a part of the amygdaloid complex.

The neostriatum (*neostr.*, figs. 15 to 25) forms the major portion of the striatum complex and extends as a part of the dorso-lateral wall of the olfactory stalk to the most caudal limit of the telencephalic evagination. It fills the lateral ventricle almost completely, and protrudes medially far above the paleostriatum. It is composed of three layers of cells, the inner and much thinned matrix (*mat.*, fig. 21), a middle layer (*mid. l.*, fig. 21) which appears to be continuous with mantle layer of the pallium proper, and an outer scattered group of cells. The latter appear to be of the same variety of cell types as those which com-

pose the paleostriatum. In the rostral extent of this ridge, that is, anterior to the levels of the di-telencephalic union, the middle layer of this area appears to correspond to the intermediate cell layer of the mantle zone of the cortical layer of the pallium. In its caudal extent, however, this same neostriatal layer appears to be in direct continuity with the cortical layer of the pallium. This layer forms a distinct band or row of cells only in its central region. Both anteriorly and posteriorly, it is broken into groups which, although they show the same dark blue staining in hematoxylin and bear the same relation to the ventricular contour of the neostriatum as the central portion does, nevertheless cannot be considered a cortical layer by any stretch of the imagination, as the former have been described.

The pyriform lobe. The pyriform lobe (*pyr. l.*, figs. 15 to 25) and lateral olfactory nucleus (*nuc. olf. lat.*, figs. 16 to 22) occupy the most lateral border of the neostriatal complex. In the anterior levels (fig. 15) it is difficult to differentiate the two, since they appear as a group of cells lateral to the neostriatum. Slightly posterior (fig. 16) these cells may be divided into a dorsal layer which is a continuation of the pallial layer and a ventral nucleus, whose ventral limit may be fixed by passing a plane through the sulcus interstriaticus and the dorsal extent of the lateral olfactory tract. This division into two parts is particularly diagrammatic in the right hemisphere in figure 17. In the region of the massive part of the di-telencephalic union, the lateral olfactory nucleus, as a small insignificant group of cells just dorsal to the lateral olfactory tract, is most marked (*nuc. olf. lat.*, figs. 19, 21 and 22). Moreover at these levels the pyriform lobe, if it has a cortical structure at all, must lie in that part of the telencephalic layer which is continuous with the main layer of the pallium dorsally and the middle layer of the neostriatum ventrally. There is no method for adequate differentiation between the pyriform and the nucleus olfactorius lateralis in these levels (figs. 23 to 25) other than the obvious fact that the more ventral part of the formation is probably nucleus.

In the extreme ventro-lateral corner of posterior portion of the telencephalic evagination a triangular nucleus is found. It

For the purposes of the present discussion, the writer has followed Kappers' classification of the striatal complex into paleostriatum, neostriatum, and archistriatum or amygdaloid complex. The paleostriatum is the ancient portion of the striatum in which various types of impulses were synthesized and discharged into the hypothalamus, subthalamus or midbrain. The neostriatum is that portion of the striatum of which the characteristic connections are neothalamic. The archistriatum is that area in the ventro-lateral wall other than the pyriform cortex and its associated lateral olfactory nucleus, into which secondary or tertiary olfactory impulses discharge and from which the olfactory projection tract originates. In Sphenodon, however, the neostriatal ridge contains the olfactory and non-olfactory portions, or the archistriatum and neostriatum respectively. In the developing telencephalon of this reptile, the paleostriatum grows more rapidly in the early stages, while later the neostriatal ridge outstrips the more ancient elevation so as to become the prominent ventricular feature of the forebrain.

The paleostriatal ridge in Sphenodon shows little differentiation. In its more rostral part it contains a group of large triangular cells arranged about fascicles of fibers which seem to become a part of the lateral forebrain bundle and with it may be distributed to the hypothalamus. Gisi ('07) described such a bundle, the tractus strio-hypothalamicus. Besides this there are smaller cells, which make up the bulk of this area and can be distinguished from the nucleus accumbens of Kappers. The latter is more clearly visible in the later stages of development than in the adult (compare figs. 4 and 6 with 9 and 12), and in that particular resembles the same nucleus in the developing paleostriatum of man. In the developing ventro-lateral wall of man, the ventricular portion becomes incorporated into the nucleus caudatus, while that portion lying beneath becomes the globus pallidus. The relation of the latter to the surrounding structures, its larger triangular cells and its contribution of fibers to the lateral forebrain bundle makes it similar to part of Johnston's caudate nucleus ('15) or his bed of the stria terminalis ('23), Crosby's ('17) small-celled ventro-lateral area, the ancient nucleus basalis

region of De Lange ('11) and Kappers (08, '21), and the ventro-lateral quadrant of Herrick's ('10, '21) studies on the forebrain of amphibians

The neostriatum proper in Sphenodon is the anterior division of the neostriatal ridge and is connected with the thalamus through the lateral forebrain bundle The fibers of this tract penetrate the irregular nuclear mass of its core and cannot be traced to the so called cortical layer This ridge develops as an enormous proliferation of the initial groups of cells which emigrate from the matrix layer The so called cortical layer develops later as a secondary separation from this nuclear mass and becomes continuous with the pyriform cortex secondarily around the sulcus superstriaticus The marked extension of this ridge into the ventricle is the product of active proliferation of neuroblasts within the core, plus an increase in the supporting tissue These cells lie between the lower extremity of the pyriform cortex and the inner layer of the neostriatum It is not due, then, to proliferation of cortical layers inward but rather to greater energy potentialities of the area opposite the lowermost edge of the pyriform This derivation cannot be spoken of as cortical, unless all the tissue which forms the striatum over and above its most ancient components, which do develop from what seems to be an area in the ventricular side opposite the pyriform cortex dorsal to the nucleus interstriaticus, be of cortical origin If, however, all tissue dorsal to the plane passed from the sulcus interstriaticus of Sphenodon or the homologous sulcus in other reptiles to the ventral limit of the pyriform be cortical this neostriatum can be thought of as cortical in origin Here there is no proliferation or inbending of general pallial areas, which become included secondarily within this large ventricular mass as described by Crosby for the alligator Here it is rather a development in situ Nor, on the other hand, can it be justly said that the origin of this new striatal tissue is striatal in the sense of De Lange and Kappers It is rather, new and as such develops in certain definite relations to the more ancient cell masses and fiber systems This is all that can be said, except as it is possible to determine the point or position in which the

rostral. The cells migrate from the matrix of that area in the same manner as they do anteriorly. Nevertheless, it is the caudal portion which is connected with the anterior olfactory area, which shows no regular inner layer and is coextensive with the nucleus ventro-medialis. If the last fact denote an origin for the posterior division of the neostriatum different from its anterior, and it is not coextensive with this nucleus, then Johnston's ('23) distinction of origin of the two parts of the dorsal ventricular ridge may apply to Sphenodon. If such be not the case, and both parts are derived from matrix lying opposite the pyriform they cannot be distinguished here by origin. However this may be, their adult relationship and fiber connections are sufficient to warrant Johnston's distinction between the two portions of the neostriatal ridge.

THE SUMMARY

1. The primitive hippocampus can be distinguished from the remainder of the telencephalic evagination in developing Sphenodon at Stage N, by an outer cell-free marginal velum. This tissue lies upon the dorsal surface in Stage N. Later in development it occupies the dorso-medial division of the hemisphere. The former stage of differentiation is a period of development of the telencephalon which resembles that of a human embryo 11.8 mm. in length, no. 1290, or that of a 9 mm. human, no. 163 mentioned by the author in 1922. There is a small undifferentiated primordium hippocampi.

2. The telencephalon medium in this reptile contains a broader piece of the ependymal tissue than that found in man. The paraphysis and its pouch are especially well developed. The pars crassa of the lamina terminalis encroaches upon the pars tenuis in growth. The growth of the former provides a bed for the anterior and hippocampal commissures.

3. The septum grows thicker as the medial and lateral septal nuclei are differentiated at the expense of the matrix. The nucleus accumbens is very prominent in Stages R and S.

4. The neopallium or general pallium is found probably between the pyriform and hippocampus, the region from which arise the tangential fibers.

5. The ventro-lateral area of the cerebral vesicle in Sphenodon, the corpus striatum, is separated from the general pallium above by a ventricular sulcus, known as the sulcus superstriaticus, and below from the septum by the angulus ventralis. This area is further divided into two ventricular ridges, a dorsal and a ventral, the neostriatum and paleostriatum respectively by the sulcus interstriaticus. In the earlier stages of growth the latter is greater and for a short period (Dendy's Stages O, OP, and Q) seems to eclipse the dorsal ridges. However, after Stage P the neostriatum begins a period of marked acceleration, which ceases only upon the completion of growth.

Within the paleostriatum no discrete nuclei are found. Fibers which join the more medial fascicles of the lateral forebrain bundles may be traced from these cells.

The neostriatum may be divided into the following cellular groups; the intermediate cell mass or layer, capped by a stratified layer, Elliot Smith's 'cortical' layer, which may be further divided into an anterior and a posterior region, and the ventro-medial nucleus of Crosby, which at the ventro-posterior pole of the telencephalon joins an irregular group of cells lying ventral to the medial limit of the stratified layer. The posterior region of the neostriatal ridge and the ventro-medial nucleus of Crosby form the archistriatum.

The intermediate layer of the neostriatum is characterized by two types of fibers, the lateral forebrain bundle connects its anterior part with the thalamus and the tractus bulbo-epistriaticus connects its posterior portion with the olfactory bulb. The ventro-medial nucleus of Crosby sends fibers into the olfactory projection tract and the stria medullaris. It may receive impulses from the lateral olfactory nucleus and the pyriform lobe.

6. The pyriform lobe cortex and the lateral olfactory nucleus are connected with the lateral olfactory tract, with the stria medullaris, the diagonal band and probably with the ventro-medial nucleus of Crosby.

As a layer of cells, the cortex of the pyriform lobe is continuous anteriorly with the general pallium; in the middle portion of the telencephalon with the so-called cortical layer of the neostriatum and ventrally with the nucleus of the lateral olfactory tract.

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PLATES

ABBREVIATIONS

Alv, alveus
Ang vent, angulus ventralis
C a, commissura anterior
C.ab, commissura aberrans
C hab, commissura habenularis
C hip, commissura hippocampi
C mam, corpus mamillare
Corp str, corpus striatum
Diag b B, diagonal band of Broca
Dien, dienecphalon
Di tel gr, di telencephalic groove
Dors s, dorsal sac
Ep ev, epiphyseal evagination
Fis endorh, fissura endorhinalis
Fis hip, fissura hippocampi
For int, foramen interventriculare
Fis rh, fissura rhinalis
For, fornix
For M, foramen Monroi
Gen pal, general pallium
Hab, habenula
Hip, hippocampus
Hyp a l, hypophysis anterior lobe
Inf, infundibulum
Lam term, lamina terminalis
Lat f b, lateral forebrain bundle
Lat t, lateral ventricle
Man l, mantle layer
Mat, matrix
Med f b, medial forebrain bundle
Mesen, mesencephalon
Mid l, middle layer
Neostr, neostriatum
Neopal, neopallium
Nuc ac, nucleus accumbens of Kappers
Nuc c al, nucleus commissurae aberrantis
Nuc com hip, nucleus commissurae hippocampi
Nuc hip com, nucleus hippocampi commissurae
Nuc let hypoth, nucleus lateralis hypothalamicus
Nuc lat sept, nucleus lateralis septi
Nuc magnoc, nucleus magnocellularis
Nuc med sept, nucleus medialis septi
Nuc olf lat, nucleus olfactorius lateralis
Nuc peric, nucleus pericentricularis
Nuc preop, nucleus preopticus
Nuc vent med, nucleus ventro-medialis of Crosby
Op ch, optic chiasma
Op ch b, optic chiasma bed
Op ev, optic evagination
Paleostr, paleostriatum
Par ar, parophyseal arch
P c, pars cerebralis
Pl ch v lat, plexus choroideus ventriculi lateralis
P of R, pouch of Rathke
P p, parophyseal pouch
Prim hip, primordium hippocampi
P t, pars tenuis
Rec op, recessus opticus
Rec preop, recessus preopticus
Rec postop, recessus postopticus
Rec mam, recessus mamillaris
Sept, septum
Sul dors, sulcus dorsalis
Str med, stria medialis
Str term, stria terminalis
Sul interstr, sulcus interstriaticus
Sul lim hip, sulcus limitans hippocampi
Sul med vent, sulcus medio-ventralis
Sul superstr, sulcus superstriaticus
Sul ver t ant, sulcus ventro-anterior
Tang f, tangential fibers
Tel, telencephalon
Tel r pl, telencephalic roof plate
Thal, thalamus
Tr bulbo-epi, tractus bulbo-epistriatus
Tr cort parolf, tractus cortico-parolfactorius
Tr lat ped, tractus habenulo-peduncularis
Tr olf lat, tractus olfactorius lateralis
Tr parolf cort, tractus parolfactorio-corticalis
Tr strio-hypo, tractus strio-hypothalamicus
Tr t bulb cort, tractus tuberculo-olfactorius
Vel transv, velum transversum

PLATE 4

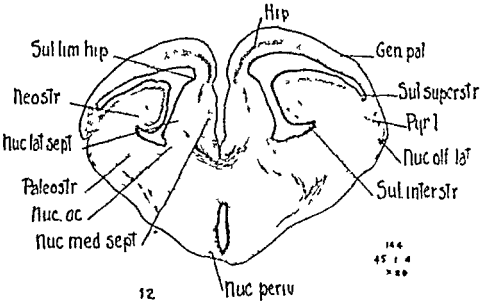
EXPLANATION OF FIGURES

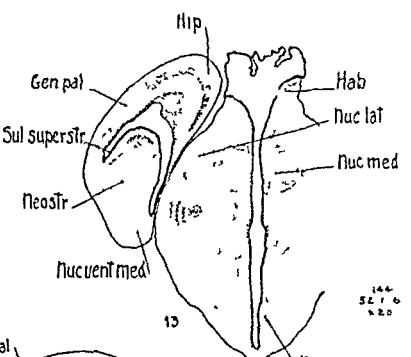
12 and 13 Transverse sections through the telencephalon of embryo no. 144, stage R.

12 Through the lamina terminalis and the septum. × 20.

13 Through the thalamus and the posterior part of the telencephalic vesicle. × 20.

14 A longitudinal section through the telencephalon of embryo Sii, stage R, which shows the difference in the anterior and the posterior arrangement of the cortex-like layer of the neostriatum. × 20.


Hip
Sul lim hip
Gen pal
Neostr
Sul superstr
Pyrl
Nuc lat sept
Nuc olf lat
Paleostr
Sul interstr
Nuc. ac
Nuc med sept
Nuc periv
12


Hip
Gen pal
Hab
Nuc lat
Sul superstr
Nuc med
Neostr
Nuc vent med
Nuc periv
13

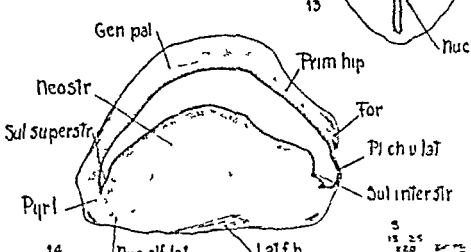
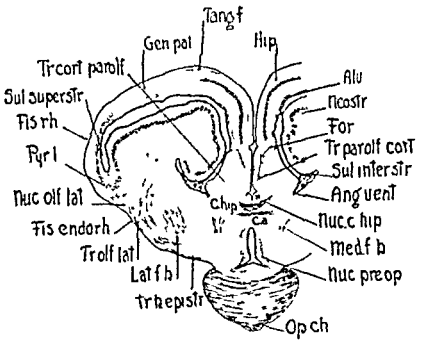

Gen pal
Prim hip
Neostr
For
Sul superstr
Pl ch v lat
Sul interstr
Pyrl
Nuc olf lat
Lat f b
14

PLATE 6

EXPLANATION OF FIGURES

19 Through the septum, the hippocampal commissure and the optic chiasma
20 Through a level slightly posterior to that of figure 19.


Tang f
Gen pal
Hip
Tr cort paralf
Sul superstr
Fis rh
Pyr l
Nuc olf lat
Fis endorh
Trolf lat
Lat f h
Tr hepistr
Alu
Neostr
For
Tr paralf cort
Sul interstr
Ang uent
Chip
Ca
Nuc c hip
Med f b
Nuc preop
Op ch
19
37 x 6 x 10

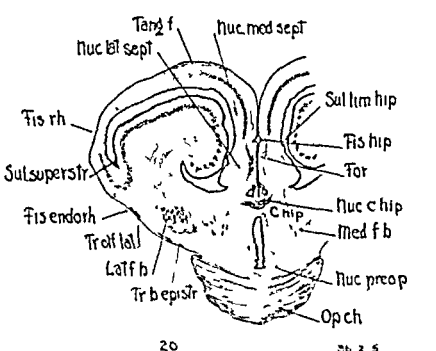

Tang f
Nuc med sept
Nuc lat sept
Sul lim hip
Fis rh
Fis hip
Sulsuperstr
For
Fis endorh
C hip
Nuc c hip
Trolf lat
Med f b
Lat f h
Tr hepistr
Nuc preop
Op ch
20
36 x 5 x 10

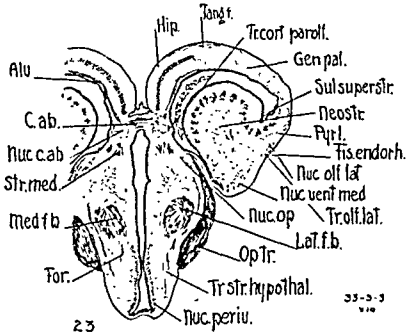
PLATE 8

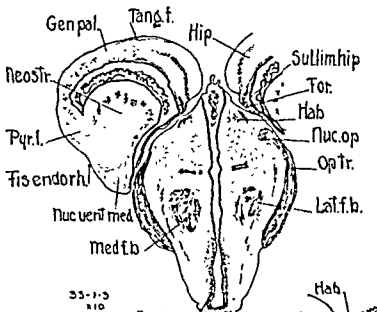
EXPLANATION OF FIGURES

23 Through the commissura aberrans and the diencephalon posterior to the foramen. The nucleus ventro-medialis and the nucleus of the lateral olfactory tract seem coextensive.

24 Through the telencephalon and the diencephalon, posterior to the di-telencephalic junction.

25 Through the most posterior end of the telencephalon and the central part of the diencephalon. In the latter division of the brain, the medial and lateral nuclei as well as the habenula may be seen.


Hip.
Tang.f.
Trcort paroll.
Gen.pal.
Alu
Sulsupersilr.
Neostr.
C.ab.
Pyr.l.
Nuc.c.ab
Fis.endorh.
Str.med.
Nuc olf lat
Nuc.vent med
Med.f.b.
Nuc.op
Tr.olf.lat.
Lat.f.b.
Op.Tr.
Tor.
Tr.str.hypothal.
Nuc.periv.
23


Gen.pal.
Tang.f.
Hip.
Neostr.
Sul.lim.hip
Tor.
Hab
Pyr.l.
Nuc.op
Op.Tr.
Fis.endorh.
Nuc.vent med
Lat.f.b.
Med.f.b.
Nuc.periv.
24

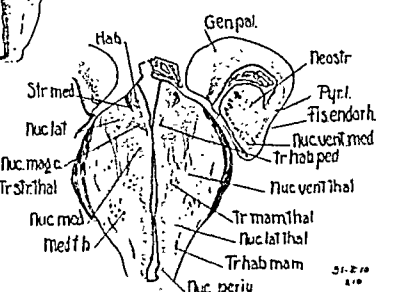
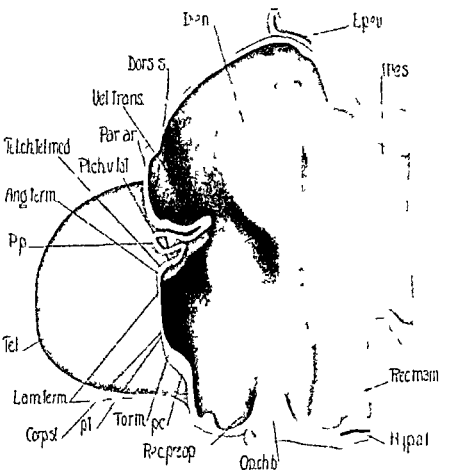

Hab
Gen.pal.
Neostr
Str.med
Pyr.l.
Fis.endorh.
Nuc.lat
Nuc.vent.med
Nuc.mag.c.
Tr.hab.ped
Tr.Str.thal
Nuc.vent.thal
Nuc.med
Tr.mam.thal
Med.f.b
Nuc.lat.thal
Tr.hab.mam
Nuc.periv
25

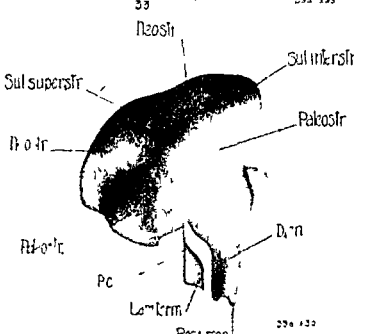
PLATE 12

EXPLANATION OF FIGURES

33 The medial sagittal aspect of the forebrain.

34 The lateral wall of the telencephalon, as seen from the ventricle, showing the paleostriatum and the neostriatum. The medial wall has been removed with the exception of that attached to pars crassa of the lamina terminalis.


Dien
Epeu
Dors S.
Hres
Vel Trans.
Par ar
Telchelmed
Pichvlat
Angterm
Pp
Tel
Lamterm
Corpst
pl
Torm
pc
Recpreop
Opchb
Recmam
Hipal
33


Neosfr
Sulinfersfr
Sulsupersfr
Paleosfr
Pedfr
Dien
Rhinfr
Pc
Lamterm
Recpreop
34

LARSELL, O. The ganglia, plexuses, and nerve-terminations of the mammalian lung and pleura pulmonalis . . 97
Latero-sensory canals of the Plagiostomi. On certain features of the . . 1
LEWIS, FREDERIC T. The significance of the term *hippocampus* . . 213
Lung and pleura pulmonalis. The ganglia, plexuses, and nerve-terminations of the mammalian . . 97

MACACUS rhesus. Anatomical studies on the motor cortex of . . 67
MALONE, EDWARD F. The cell structure of the superior olive in man . . 205
Mammalian lung and pleura pulmonalis. The ganglia, plexuses, and nerve-terminations of the . . 97
Man. The cell structure of the superior olive in . . 205
Man. The subdivisions of the neural folds in . . 231
Motor cortex of Macacus rhesus. Anatomical studies on the . . 67

NAÑAGAS, JUAN C. Anatomical studies on the motor cortex of Macacus rhesus. . . 67
Nerve-terminations of the mammalian lung and pleura pulmonalis. The ganglia, plexuses, and . . 97
Nervous system of arachnids: scorpions, phalangids, and trap door spiders. Further notes on the central . . 249
Nervus trigeminus in the albino rat. On bilateral effects from the unilateral section of branches of the . . 133
. the . . 231
. rom the unilateral section of branches of the nervous trigeminus in the albino rat . . 133

OLIVE in man. The cell structure of the superior . . 205

PARATHYROIDECTOMY at 100 days of age on the growth of the brain and spinal cord of male and female albino rats. Studies of the thyroid apparatus. XII. The effect of thyro-parathyroidectomy and . . 313
Phalangids, and trap door spiders. Further notes on the central nervous system of arachnids: scorpions . . 249
Pigeon. A note on the excitable areas of the cerebral hemispheres of the . . 61
Pigeon as related to various instinctive types of behavior. Studies of the brain stem. VI. An experimental study of the corpus striatum of the . . 21
Pig. Origin and destination of the secondary visceral fibers in the guinea . . 275
Pig. Origin and distribution of the tractus solitarius in the guinea . . 171
Plagiostomi. On certain features of the latero-sensory canals of the . . 1
Pleura pulmonalis. The ganglia, plexuses, and nerve-terminations of the mammalian lung and . . 97
Plexuses, and nerve-terminations of the mammalian lung and pleura pulmonalis. The ganglia . . 97
Pulmonalis. The ganglia, plexuses, and nerve-terminations of the mammalian lung and pleura . . 97
Pupillae and the sympathetic. The dilatator . . 163

RAT. On bilateral effects from the unilateral section of branches of the nervus trigeminus in the albino . . 133
Rats. Studies of the thyroid apparatus. XII. The effect of thyroparathyroidectomy and parathyroidectomy at 100 days of age on the growth of the brain and spinal cord of male and female albino . . 313
Reflexes of spinal frogs as induced by chemical stimulation . . 15
ROGERS, FRED T. A note on the excitable areas of the cerebral hemispheres of the pigeon . . 61
ROGERS, FRED T. Studies of the brain stem. VI. An experimental study of the corpus striatum of the pigeon as related to various instinctive types of behavior . . 21

SCORPIONS, phalangids, and trap door spiders. Further notes on the central nervous system of arachnids. . . 249
Section of branches of the nervous trigeminus in the albino rat. On bilateral effects from the unilateral . . 133
Solitarius in the guinea pig. Origin and distribution of the tractus . . 171
Sphenodon punctatum. The development of the telencephalon in . . 483
Spiders. Further notes on the central nervous system of arachnids: scorpions, phalangids, and trap door. . . 249
Spinal cord of male and female albino rats. Studies of the thyroid apparatus. XII. The effect of thyro-parathyroidectomy and parathyroidectomy at 100 days of age on the growth of the brain and . . 313
Spinal frogs as induced by chemical stimulation. Reflexes of . . 15
Stem. VI. An experimental study of the corpus striatum of the pigeon as related to various instinctive types of behavior. Studies of the brain . . 21
Stimulation. Reflexes of spinal frogs as induced by chemical . . 15
Striatum of the pigeon as related to various instinctive types of behavior. Studies of the brain stem. VI. An experimental study of the corpus . . 21
Structure of the 205
Superior olive in 205
Sympathetic. T 163
System of arachnids: scorpions, phalangids, and trap door spiders. Further notes on the central nervous . . 249

TELENCEPHALON in Sphenodon punctatum. The development of the . . 483
Thyroid apparatus. XII. The effect of thyro-parathyroidectomy and parathyroidectomy at 100 days of age on the growth of the brain and spinal cord of male and female albino rats. Studies of the . . 313
Thyro-parathyroidectomy and parathyroidectomy at 100 days of age on the growth of the brain and spinal cord of male and female albino rats. Studies of the thyroid apparatus. XII. The effect of . . 313
Tractus solitarius in the guinea pig. Origin and distribution of the . . 171
Trigeminus in the albino rat. On bilateral effects from the unilateral section of branches of the nervus . . 133
Types of behavior. Studies of the brain stem. VI. An experimental study of the corpus striatum of the pigeon as related to various instinctive . . 21

UNILATERAL section of branches of the nervus trigeminus in the albino rat. On bilateral effects from the . . 133

VISCERAL fibers in the guinea pig. Origin and destination of the secondary . . 275

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